Tell me what you do:

The neural processing of the language-action interrelation

in early language development

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Abstract

We communicate by means of language and actions, which we represent in our cognitive system (i.e., action representations). Communication is successful if interaction partners understand each other. This doctoral thesis studies the contribution of the mirror neuron system to the processing of communicative signals in early language development. Two studies investigated if and how the mirror neuron system processes communicative signals (i.e., actions and language) in 18-24-month-olds. Both studies assessed the activity of the mirror neuron system (MNS) by electroencephalography (EEG). Study 1 showed that the mirror neuron system is involved in processing action-related language, specifically action verbs. To do so, it takes the role of a prediction system, which was demonstrated by Study 2, in which action prediction was enhanced if corresponding linguistic information was present previously. In conclusion, the findings of this doctoral thesis point to an involvement of the mirror neuron system in processing communicative signals early in language development by making predictions. Furthermore, it was shown that action and language are interrelated.

Zusammenfassung

Wir kommunizieren mittels Sprache und über Handlungen, welche wir kognitiv repräsentieren (d.h. Handlungsrepräsentationen). Kommunikation ist erfolgreich, wenn sich Interaktionspartner verstehen. Diese Promotionsarbeit befasst sich damit, was das Spiegelneuronensystem zur Verarbeitung von kommunikativen Signalen in der frühen Sprachentwicklung beiträgt. In zwei Studien wurde untersucht, ob und wie das Spiegelneuronensystem von 18-24-Monatigen kommunikative Signale (d.h. Handlung und Sprache) verarbeitet. Die Aktivität des Spiegelneuronensystems wurde in beiden Studien mittels Elektroenzephalographie (EEG) erhoben. Studie 1 zeigte, dass das Spiegelneuronensystem an der Verarbeitung von handlungsbezogener Sprache, insbesondere Handlungsverben, beteiligt ist. Dabei nimmt es die Rolle eines Vorhersagesystems ein, was Studie 2 zeigte, denn Handlungsvorhersagen waren erleichtert, wenn zuvor die passende sprachliche Information vorhanden war. Zusammenfassend weisen die Befunde dieser Promotionsarbeit darauf hin, dass das Spiegelneuronensystem schon in der frühen Sprachentwicklung durch Vorhersagen an der Verarbeitung von Kommunikation teilnimmt. Zudem zeigte sich, dass Handlung und Sprache miteinander in Verbindung stehen.

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Part I

1. Introduction

Imagine a parent and a two-year-old toddler at playtime. They are playing with modeling clay of different colors. At one point the parent says. “I want to cut some shapes”, pointing at the yellow modeling clay. The toddler looks at the modeling clay and then to the cutters of different shapes next to him. The toddler hands the star-shaped cutter to the parent. “Thank you! Let’s cut some stars then“, says the parent. While the parent gets hold of the cutter, the toddler’s eyes are already impatiently resting on the modeling clay waiting for the parent to place the cutter and transform the yellow mass into nice stars.

In this example, we witness a social interaction between a parent and a toddler. The parent communicates the next step of working the modeling clay by using language, and somehow the toddler seems to understand what the parent is saying because he anticipates the request for the cutter hearing the verb “to cut” and hands the cutter over. The toddler adapts his behavior to the requirements of this social interaction and communicates through actions (i.e., goal-directed movements; von Hofsten, 2004). Moreover, the toddler seems to have a concept of cutting shapes because he knows what will happen after the parent has grasped the cutter.

In the current dissertation project, I aimed to investigate how different forms of communicative signals (i.e., actions and language) are processed in early development, so that successful social interactions are enabled as in the introductory example. Early development, or more specifically toddlerhood, is of special interest because verbal communication starts to develop (Bates et al., 1994), which allows us to study communicative signals from different modalities as they develop. I was particularly interested in the question whether communicative signals from different modalities are processed similar to each other in the brain of toddlers. Furthermore, I aimed to investigate if communicative signals are interrelated with each other on a neural level (i.e., interaction of processing).

Social interactions consist of a coordinated exchange of communicative signals between interaction partners (Rączaszek-Leonardi, Nomikou, Rohlfing, & Deacon, 2018). Therefore, successful social interactions require that interaction partners understand each other and adapt their behavior appropriately. Understanding refers to processing the *how, what, and why* of communicative signals (Thioux, Gazzola, & Keysers, 2008). Humans use many different forms of communicative signals in their interactions with others, such as actions (i.e., goal-directed movements; von Hofsten, 2004), gestures (Bates & Dick, 2002), and language (Tomasello, 2003). In the introductory example, the parent used a pointing gesture to direct the toddler's attention to the subject of interest. Then, the intended action was communicated verbally. Finally, the parent cut the modeling clay (goal-directed action) communicating that the intended action is executed. Furthermore, in this interaction, the toddler also used a goal-directed action (handing the cutter) to communicate that he had understood the intended action of the parent. The question is how these two people understand each other's pointing, acting, and talking, that is, *how* are they communicating (i.e., pointing, acting, talking), *what* are they communicating (i.e., goal or meaning), and *why* are they communicating (i.e., higher-order intention)?

Rizzolatti and Craighero (2007) put it quite simply; interaction partners need to share a representation of their communicative signals in order to understand them. In general, representations are mental entities which stand for something ("Mental representation," n.d.). Thereby, they are the units with which cognitive operations are performed. For instance, one can have a representation of an action, that is, a mental entity, which stands for what the action means, why, how, and on what object an agent performs it (e.g., parent uses cutter to divide modeling clay into stars to decorate the house). Similarly, representations for a word stand for the context in which it is used and what it refers to (e.g., "cutting" refers to the application of the cutter on the modeling clay). However, the question is, when we see the first signs of representations for communicative signals in development.

Evidence shows that infants represent actions already by the age of 3 months (Luo, 2011). This means that infants perceive actions performed by others as guided by goals (Daum & Gredebäck, 2011; Daum, Prinz, & Aschersleben, 2008, 2011; Daum, Vuori, Prinz, & Aschersleben, 2009; Luo & Johnson, 2009; Woodward, 1998). Thus, they represent on what object an agent performs an action. It has been suggested that the development of action-goal representations is not a purely cognitive process but linked to motor development. This is because the perception of goal directedness is associated with infants' first-hand experience with grasping actions (Kanakogi & Itakura, 2011; Sommerville, Woodward, & Needham, 2005). Ascribing goals to the actions of others might be only a rudimentary form of cognitively representing an action because people who are performing actions do not only have goals but also intentions. Intentions are a conglomerate of the means to achieve a goal (e.g., holding the cutter with the arm outstretched) and the goal itself (e.g., showing the cutter, handing the cutter over, requesting help to handle the cutter; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Representing the actor's intention thus refers to how and why an action is performed. Because people make their intentions available to others by performing actions, actions are communicative signals. However, we do not only use actions to make our intentions available, but we use gaze or gestures (Tomasello et al., 2005). Gestures are prominent signals in communication, and 4-5-month-old infants show an early sensitivity for the direction of pointing gestures, indicated by their shift of attention in the direction of a pointing hand (Rohlfing, Longo, & Bertenthal, 2012). Pointing gestures are also the first type of gestures which are produced by infants in ontogenetic development, at around 9-12 months of age (Brooks & Meltzoff, 2008). Furthermore, perceiving pointing gestures as communicative cues which indicate a person's mental state (e.g., the person wants to communicate something about a particular object) also emerge at around 9-12 months of age (Woodward & Guajardo, 2002), despite an early sensitivity towards pointing gestures as described above. This means that the perception and production of pointing gestures as communicative signals are interrelated, and, furthermore, that the cognitive representation of pointing gestures is associated to the motor production of the latter. So, when an infant starts to point, he also has a representation of what it means when someone points and what the intention of this person is. It is not surprising that the ability to perceive gestures as communicative cues and the ability to produce gestures to direct others' attention goes hand in hand with a milestone in cognitive development: joint attention. Joint attention refers to sharing an experience and knowing that one is sharing it with the interaction partner (Tomasello, 1995). Furthermore, joint attention is important for communication and successful social interactions because it allows infants represent the mental state of the interaction partner and compare it to their own mental state (Tomasello & Carpenter, 2007). If the two mental states are not matching, the infant will start to use communicative signals such as pointing to alter the mental state of the interaction partner (Legerstee & Barillas, 2003; Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004; Liszkowski, Carpenter, & Tomasello, 2007; Woodward & Guajardo, 2002). Moreover, infants start to share their experiences and mental states by using their first words. Thus, the language domain of communicative signal emerges (i.e., becomes explicitly perceivable to an interaction partner). In most languages, infants start to use nouns that represent concrete entities (Childers & Tomasello, 2006; Kuhl, 2004). Only between 18 and 24 months of age, they start to acquire verbs that represent events and processes (Golinkoff & Hirsh-Pasek, 2008), while action-based communicative signals are represented much earlier. This means that the toddler in the initial example just learned what it means when the parent says, "to cut" but has already known for more than a year that the described action is goal-directed. Does this mean that representations of language develop based on representations of actions? Bruner (1964) agreed with this and proposed a step-wise development of cognitive-perceptual representations and language. In this step-wise development, perceptual/sensorimotor representations and cognitive representations are the basis for language representations

(Bruner, 1964). Therefore, an interrelation between cognition, perception, and language is proposed (for a similar view see Barsalou, 2008). Furthermore, it is proposed that language representations derive from early sensorimotor and cognitive representations (Bruner, 1964). In contrast, Mandler (1988) argued for a parallel development of conceptual representations (cognition and language) and sensorimotor representations. This means that there are contrasting views on the development of representations for different communicative signals. However, these views agree on a potential interrelation between language, cognition and sensorimotor representations during processing (Barsalou, 2008; Bruner, 1964; Mandler, 1988). Chomsky's perspective stands in stark contrast to this. He proposed that language is an innate capacity, which does not develop and does not relate to any other representational system (Chomsky, 2009; Jablonka, 2017). By investigating the processing of communicative signals, the current dissertation project might add to the debate of whether sensorimotor processes, cognition, and language are interrelated from early on.

To sum up, interaction partners need to share a common ground of representation to comprehend and produce human communicative signals (Tomasello, 2003). Each communicative signal from the action and the language domain reveals important information about the intentions, goals, and beliefs of the sender, which have to be represented and interpreted by the receiver in order for him to react appropriately (Tomasello, 2003).

In the following sections, I will describe how we accomplish the task of representing and processing different, potentially interrelated communicative signals by means of a specialized neural network that we are equipped with. First, I will focus on the anatomical characteristics, the ontogenetic development, and the functional properties of this network. To start with, I will concentrate on action processing, before drawing the link to language processing. Second, I will discuss the nature of the interaction between action and language because both action and language are forms of communication, which might co-occur.

1.1. Mirror neurons in the monkey brain

The neural network that is involved in processing actions comprises a special type of neurons, called mirror neurons. Mirror neurons were first discovered in macaque monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). It has been shown that a part of the premotor cortex of macaque monkeys, area F5, comprises a type of neurons that fire when an action is executed by the monkey himself (e.g., grasping for a peanut) but also when the monkey observes another monkey or a human performing the same action (di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001; Umiltà et al., 2001). These findings were interpreted as the neural underpinnings for action understanding, that is, deriving action goals from observed actions (Rizzolatti & Craighero, 2004). Additional to area F5, research has demonstrated that the inferior parietal lobule and the primary motor cortex comprise mirror neurons as well (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Tkach, Reimer, & Hatsopoulos, 2007). It has been suggested that parietal mirror neurons code for the intention of an action, that is, does someone grasp the peanut to eat it or to place it into a container (Fogassi et al., 2005)?

1.2. Mirror neurons in the human brain

The discovery of mirror neurons in monkeys was a milestone for research of human social functions. In the past two to three decades, the mirror neuron system (MNS) has been extensively studied in humans to inform us about important social functions, such as action understanding, empathy, theory of mind, and imitation (Decety, 2010; Iacoboni et al., 2005; Rizzolatti & Craighero, 2004). However, for more than ten years and in contrast to monkey studies, there was no direct evidence for the existence of mirror neurons in humans. This was changed by a study which used the same measurement techniques to record mirror neuron activity in human patients as in the original studies with monkeys (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). This study recorded extracellular potentials of single neurons intracortically while patients performed and observed actions. It was demonstrated that humans and not only monkeys have neurons with mirroring properties. Specifically, these neurons were found in the supplementary motor area, the hippocampus, the parahippocampal gyrus, and the entorhinal gyrus of the human patients. However, this study did not record activity from lateral frontal sites as in macaque monkeys (Mukamel et al., 2010). This means that there is no direct evidence for mirror neurons in the human premotor cortex analogous to the monkey area F5. Other studies using indirect measures (i.e., functional magnetic resonance imaging, magnetoencephalography, electroencephalography) report mirroring activity in the inferior frontal gyrus, the inferior parietal lobule, and the superior temporal sulcus (for a review see Rizzolatti & Craighero, 2004). Furthermore, Pineda (2008) pointed out that this core MNS is strongly interconnected with an extended MNS comprising sensorimotor cortices, dorsal portions of the premotor cortex, and the medial temporal gyrus.

Functionally, the MNS has similar properties in humans as in monkeys, that is, the observation and execution of actions are associated with activation of the MNS in adults, children, toddlers, and infants from 8 months of age (Fox et al., 2016; Gastaut, 1952; Hari et al., 1998; Hari & Salmelin, 1997; Hobson & Bishop, 2016; Marshall, Bar-Haim, & Fox, 2002; Muthukumaraswamy, Johnson, & McNair, 2004; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Warreyn et al., 2013). Rizzolatti and colleagues (2001) claimed that the MNS is the tool with which actions are understood (i.e., goals and intentions are derived) because it directly maps an observed action onto the observer's motor program, required for performing the action (i.e., direct-matching account). This is in line with studies in adults as well as in infants which claimed that the MNS only codes for goal-directed movements (Hobson & Bishop, 2016; Marshall, Saby, & Meltzoff, 2013; Muthukumaraswamy et al., 2004; Nyström et al., 2011; Southgate, Johnson, Karoui, & Csibra, 2010). This means that the MNS is active, when a goal can be derived. It has, for instance, been shown that non-transitive opening and closing of an empty hand was not related to MNS activity, while it was for opening and closing a hand holding a pencil (Hobson & Bishop, 2016). In that sense, mirroring is at least object-specific. However, other studies claim that goal- or object-directedness is not necessary for the MNS to react (Virji-Babul, Rose, Moiseeva, & Makan, 2012; Warreyn et al., 2013).

A further important characteristic, especially for developmental populations, is the experience dependency of MNS activity. Studies in adults, using functional magnetic resonance imaging (fMRI), have shown that the MNS is more active when an action is observed for which the observer has high expertise (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Similarly, highly familiar actions are associated with more MNS activity than less familiar actions (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Liew, Sheng, Margetis, & Aziz-Zadeh, 2013). Importantly, also completely novel actions seem to be related to MNS activity measured with electroencephalography (EEG; Liew et al., 2013). In infants, studies using EEG have demonstrated that the MNS is more active for actions that the infants already have in their own motor repertoire. For instance, infants who are good crawlers but do not walk yet (or have only recently learned to walk) display more MNS activity towards the observation of crawling actions than walking actions (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). Similar results have been obtained for reaching and grasping competence (Cannon et al., 2015).

All this evidence was taken as basis for the proposal that the human MNS forms the neural substrate of interpreting what happens in the social world around us. It was proposed that this is achieved by mapping the actions of our interaction partners on our own motor system, thus creating a shared representational ground (Rizzolatti et al., 2001). The following section scrutinizes where the MNS comes from and if its function is a product of development.

1.3. The development of the mirror neuron system

Initially, it has been assumed that mirror neurons are innate, that is, their mirroring properties are hard-wired in our genetic code and a product of evolution (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004). This assumption was corroborated by a behavioral study showing that newborns have a preference for goal-directed actions (Craighero, Leo, Umiltà, & Simion, 2011). According to this view, mirror neurons are there from the beginning on and do not emerge but only specialize in ontogenesis. However, a preference for goal-directed actions does not provide evidence for the existence of mirroring properties at birth. In addition, such a preference does not mean that newborns interpret actions as goal-directed. Last but not least, the assumption that mirror neurons exist because of a hard-wired genetic code contradicts recent theories on cognitive and brain development. Recent developmental theories, such as neuroconstructivism, suggest that human brains and their functions develop within complex bidirectional interactions between genes, neural structures, neural functions, and the environment (Johnson & de Haan, 2015; Karmiloff-Smith, 2017; Westermann et al., 2007). These different levels are part of a mutual and self-organizing process of change (Westermann et al., 2007). This process of change is characterized by constraints from one level to the next (Westermann et al., 2007). This means that genes do not only lead to changes in neural structures, which then influence neural functions that allow to process a certain environmental input (bottom-up cascade). It also means that the environmental input shapes functions, which, in turn, change structural properties and affect gene expression (top-down cascade; Gottlieb, 2007; Johnson & de Haan, 2015). Therefore, the development of mirror neurons is not a unidirectional mechanism from gene to the functional property of mirroring but underlies a complex process constrained by interactions between genes, neural structures, neural functions, and environmental input (Johnson & de Haan, 2015). This means that the development of mirror neurons is not hard-wired but experience-expectant (Johnson & de Haan, 2015; Karmiloff-Smith, 2017; Westermann et al., 2007). Experience expectancy is the need for external input (experience), for which the system is prepared at a specific point in time (expectant; Karmiloff-Smith, 2017). This means that the external input can most efficiently shape the system in a sensitive period, which is different from adult learning in later life (Karmiloff-Smith, 1998; Quadrelli & Turati, 2016). From a neuroconstructivist perspective, it is, furthermore, important to note that the term *experience* is not restricted to external environmental input but can also comprise the interaction between the different levels of a system (e.g., a particular type of neural activity given the current neural anatomy and gene expression; Westermann et al., 2007). This is important because, in neuroconstructivism, the different levels are highly interrelated. Therefore, it makes little sense to single out the environmental input and classify it as experience.

It was put forward that one possible mechanism that experience has on the development of mirror neurons in ontogeny is associative learning when encountering co-occurrence of sensory input and motor output (Cooper, Cook, Dickinson, & Heyes, 2013; Heyes, 2010; Press, Heyes, & Kilner, 2011). Due to this co-occurrence, sensory and motor regions develop strong functional connections which ultimately allow sensory input (and observed action) to activate motor regions (Cooper et al., 2013; Heyes, 2010). It has been proposed that the neural mechanism for this associative connection is Hebbian learning (Keysers & Gazzola, 2014). Hebbian learning comprises two important principles, contiguity and contingency (Hebb, 1949). Keysers and Gazzola (2014) argue that these two principles are also proposed by the associative learning account. Contiguity is a very close temporal organization of two activities in two different cells or cell assemblies. This means that activity in two cells or cell assemblies co-occur within a very narrow time window (Keysers & Gazzola, 2014). Contingency, instead, implies causality and predictability, that is, one can predict from the activity in one cell that the other cell will be active as well, given the time window discussed before (Keysers & Gazzola, 2014). Hebb explained the learning process on the cellular level with much precision: "When an axon of cell A is near enough to excite a cell

B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased” (Hebb, 1949, p. 62). I argue that Hebbian learning is a description of a neural learning process underlying associative learning, which is the basis for the development of the MNS.

1.4. The contribution of the mirror neuron system to action understanding

Once two cell assemblies or cortical regions have started to be connected, they can function as a network. For mirroring, this means that sensory and motor regions have initially been linked, which has resulted in mirroring properties (Quadrelli & Turati, 2016). In the beginning, this network is topographically wide-spread and gets more focused and functionally tuned through experience, according to neuroconstructivism (Quadrelli & Turati, 2016; Westermann et al., 2007). However, the question remains what these mirroring properties tell us about action understanding (i.e., deriving goals and intentions).

Hebbian learning can explain how cortical areas that process sensory input (i.e., an observed grasp) and those processing motor programs connect to each other. However, an actor can have many different intentions and goals when executing a motor program (Kilner, Friston, & Frith, 2007a). An observer has therefore to be able to disentangle the different possibilities and to select the correct one in order to fully understand the actor’s action, that is, processing the means, the goals, but also the intentions (Kilner et al., 2007a). The direct-matching account has troubles dealing with this issue because it is stated that a perceiver automatically derives the intention of the actor from his or her own motor program. But which intention is correct, and does the perceived intention always correspond with the actor’s intention? Probably not (Caramazza, Anzellotti, Strnad, & Lingnau, 2014). Similarly, Hebbian learning alone cannot explain this process. Implicitly, the disentangling and selection of possible intentions and goals of an action leads to the assumption that prediction plays an important role in processing other people's actions. However, what do we exactly predict, and how do we give meaning to it?

Flanagan and Johansson (2003) suggested that action prediction and action understanding are two parallel processes taking place simultaneously. However, this poses the same problems again as the direct-matching account. In contrast, Csibra (2007) and Southgate (2013) suggested that the MNS is activated by recognition, that is, it pre-constructs or predicts the goal-achievement process, based on the action goal (and intention) which was identified outside the MNS. Indeed, studies have shown that mirroring brain activity starts before the action is completed (Southgate, Johnson, Osborne, & Csibra, 2009) and that mirroring even occurs for biologically impossible actions (e.g., human lower arm moving around objects in a snake-like manner to grasp the last object in a row; Southgate & Begus, 2013). In this case, neural mirroring is a consequence of perceiving the action goal (Csibra, 2007; Southgate, 2013). With the predictive coding account, Kilner, Friston, and Frith (2007a) and later Kilner (2011) take a position on a middle ground between the two perspectives described above. According to them, action understanding does not come with action prediction, nor is the goal solely identified and then re-enacted by the motor system. In the following paragraph, I will describe how the predictive coding account explains the perception of intentions and goals of an action.

The predictive coding account suggests that a large neural system is involved in action perception based on predictions made on various levels of the system's hierarchy (Kilner et al., 2007a). This system involves the core regions of the human MNS (premotor cortex, inferior parietal lobule, superior temporal sulcus) as well as the middle temporal gyrus (Kilner, 2011). Therefore, the predictive coding account assumes a contribution of the ventral and the dorsal stream (Kilner, 2011). The temporal lobe is known for its functions in long-term memory, thus for the storage of concepts and representations (Kilner, 2011). If we consider representations as neural activation patterns (Westermann et al., 2007), the temporal cortex stores these patterns associated with a certain stimulus, such as an observed action. The predictive coding account suggests that the hierarchically high components of an action representations, such as the intentions (i.e., long-term goal: decorating the house with stars) and action goals (i.e., short term goal: cut the stars out of modeling clay), are stored in the medial temporal gyrus (Kilner, 2011). This is in line with Tomasello's proposal (2005) that intentions are concepts including the means to achieve an action as well as the goal that wants to be achieved. Processing intentions and goals does not provide us yet with the certainty that our interpretation is correct and actually matches the intentions and goals of the actor. In order to analyze if the intentions and goals of an observed action were interpreted correctly, the medial temporal gyrus identifies a possible intention and goal behind the observed actions and generates predictions about the motor program that would be necessary to attain the goal which is passed along the MNS (Kilner, 2011). Based on the assumed motor program, the premotor cortex predicts the sensory consequences of the execution of the motor program (i.e., what does it feel like, what does it look like when I cut modeling clay) which are sent via a dorsal stream to somatosensory, parietal, and superior temporal areas of the cortex (Kilner, 2011; Kilner et al., 2007a). This is highly similar to Csibra's proposal (2007) of a top-down processing for action understanding. However, in addition, the predictive coding account specifies a bottom-up route: the lower levels compare the actual sensory input with the prediction and send the prediction error forward to the areas that are higher in the hierarchy. If these prediction errors are minimal on all levels of the hierarchy, it is highly probable that the action has been interpreted correctly, that is, the predictions were particularly good (Keysers & Gazzola, 2014; Kilner et al., 2007a). On top of this, predictive coding implies an experience-dependent flexibility of the system, arguing that prediction errors are used to update the models from which predictions are derived in the first place (Kilner et al., 2007a). Therefore, predictive coding is a data-driven process (Keysers & Gazzola, 2014; Kilner, Friston, & Frith, 2007b). One has prior expectations about the conditional probability of one event (e.g., taking a peanut with a pincer grip) given another (e.g., wants to eat the peanut; Keysers & Gazzola, 2014). These prior expectations are compared against the actual outcome (e.g., peanut was grasped with a power grip). This outcome is then used to adjust the prior expectations and to create an updated conditional probability distribution, that is, posterior expectations (e.g., using a power grip has become slightly more likely, and using a pincer grip slightly less likely; Keysers & Gazzola, 2014). Predictive coding models on a theoretical level what Tomasello and colleagues (2005) proposed about action hierarchies: top-down processing serves to answer the question *how* an intended result is obtained, while bottom-up processing serves to understand if the inferred intention was correct in the first place, so, why an action is performed. Sensorimotor activity that serves predictive and model updating functions, as proposed by the predictive coding account, is in line with empirical findings showing that infants involve their sensorimotor system to process simple goal-directed actions although the actor is not human (e.g., mechanical claw grasping an object; Southgate et al., 2010). In a direct matching perspective, non-human agents should not activate the sensorimotor system for the observation of a grasp performed by a mechanical claw because there is no motor program one can map the observed action on. Moreover, it has been shown that the sensorimotor system is active before the onset of the action (thus, before one can map any observed movement on one's motor system), which speaks for a predictive function of the sensorimotor system (Southgate et al., 2009). Furthermore, studies suggest that experience (visual or motor) with action modulates sensorimotor involvement during action observation, in such a way that more familiar actions are associated with more sensorimotor activity (Cannon et al., 2015, 2014; de Klerk, Johnson, Heyes, & Southgate, 2015; de Klerk, Southgate, & Csibra, 2016; van Elk et al., 2008; Yoo, Cannon, Thorpe, & Fox, 2016).

To sum up, the predictive coding account suggests that initial Hebbian learning results in a predictive network including the human MNS. This network enables us to understand action-based communicative signals of our interaction partners as result of the interplay between top-down and bottom-up processing. This raises the question whether this network is also involved in processing a very prominent form of communication, namely language. In the following section, I will discuss if and how the human MNS is involved in language processing.

1.5. Language processing and the mirror neuron system

It has been argued that the human MNS is critically involved in processing actions and interpersonal communication, such as language (Gentilucci & Corballis, 2006; Rizzolatti & Arbib, 1998). In line with this, Tomasello (2003) assumed that language and actions are very similar because they both serve the ultimate goal of communication and sharing intentions. From an evolutionary point of view, it has been suggested that any type of human communicative signals have developed from the ability to read the intentions of our interaction partners, to share them, and to alter the mental states of interaction partners (Tomasello, 2003; but see also Chomsky (2009) for a different perspective). Thus, Tomasello (2003) assumed that action-based and language-based communication have evolved due to a common basis: sharing experiences with others.

In a similar vein, linking action and language, Rizzolatti and Arbib as well as Corballis (1999) argue that language has developed from communicative gestures. This means that a linguistic form of communication developed directly from a non-linguistic form that served the purpose of communicating with others. These authors claim that the development of language from communicative gestures is the reason why producing hand movements and producing language share a common neural basis, namely Broca's area (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2007). It has been argued that Broca's area is a convergence zone for motor control of movements executed with the hand and the mouth (Pulvermüller, 2017). Even in nonhuman primates, area F5, of which Broca's area is potentially the human homologue, reacts to actions performed with the hand as well as with the mouth (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). It has been proposed that early language evolved from so-called mouth gestures (Gentilucci & Corballis, 2006). Research studying sign language corroborated this proposal. Mouth gestures are still present in sign language and serve to distinguish similar manual gestures (Emmorey, 2002). The mouth gestures might have gradually replaced manual gestures, and vocal language developed (Gentilucci & Corballis, 2006). This might have happened in the context of developing cultural skills such as tool use and teaching tool use to group members (Corballis, 2002). If producing vocal language has developed from producing gestures, it seems probable that language and gestures share a common system for processing, such as Broca's area.

However, embodied cognition assumes that not only Broca's area but the entire MNS is a common processing system for communicative signals from different modalities (Barsalou, 2008). It is argued that the MNS derives meaning by using the observer's motor system to process the underlying action representation (Barsalou, 2008; Fischer & Zwaan, 2008). Such an action representation does not only comprise the motor programs needed do execute an action (e.g., motor program for holding a cutter and pressing it into modeling clay) and the visual information derived from action observation (e.g., what it looks like when one cuts modeling clay with a cutter) but information from other modalities as well (e.g., auditory, linguistic; Barsalou, 2008; Fischer & Zwaan, 2008). It has been proposed that action representations also consist of auditory information (e.g., scratchy sound when cutter hits the table top after having cut the modeling clay) and/or linguistic information, such as action-related language (e.g., hearing the word "cutting" uttered by the parent; Barsalou, 2008; Fischer & Zwaan, 2008).

Action-related language includes any linguistic entity that is tightly linked to an action. Tool labels and verbs are examples for such a close relation. As tools are always linked to particular actions and action affordances, the labels are as well (Carota, Moseley, & Pulvermüller, 2012). In addition to tool labels, verbs are directly associated with actions because verbs are morphemes expressing events and processes (Golinkoff & Hirsh-Pasek, 2008). This is especially true for the so-called action verbs, such as running, drawing, or standing (Golinkoff & Hirsh-Pasek, 2008; Springer & Prinz, 2010). Action verbs can further be categorized in terms of dynamics. For instance, "running" is highly dynamic, while "standing" is highly static (Springer, Huttenlocher, & Prinz, 2012). In contrast, abstract verbs are less tightly linked to actions because they describe states or processes that are not directly visible, such as believing and existing (Golinkoff & Hirsh-Pasek, 2008; Moreno, de Vega, & León, 2013).

In ontogenetic development, toddlers start to acquire their first verbs at around 18 months of age (Bates & Dick, 2002; Maguire, Hirsh-Pasek, & Golinkoff, 2006). First verbs foremost comprise action verbs and to a much lesser extent abstract verbs (Kauschke, 2012; Maguire et al., 2006). At this age, the toddlers comprehend action verbs that are part of their daily lives. However, the expressive verb repertoire is still relatively limited (Bates & Dick, 2002; Golinkoff & Hirsh-Pasek, 2008; Sootsman Buresh, Woodward, & Brune, 2006). At around 24 months of age, the first expressive action verbs begin to emerge (Bates & Dick, 2002; Tomasello, 1992). This is also when two-word sentences become more prevalent in toddlers' language (Golinkoff & Hirsh-Pasek, 2008).

Toddlers' verb acquisition is potentially a result of associative learning (Gentner & Boroditsky, 2001; Golinkoff & Hirsh-Pasek, 2008). Specifically, when toddlers acquire new verbs, they need to represent different characteristics of the described event: the path or the manner in which an action is performed, the source and the goal of an action, as well as characteristics of containment and support (Golinkoff & Hirsh-Pasek, 2008; Mandler, 2004). By the time these characteristics are cognitively represented, the toddler can map a linguistic symbol (i.e., the action verb) on the existing action representation (Gentner & Boroditsky, 2001; Golinkoff & Hirsh-Pasek, 2008). This mapping is complex because verbs, which are static symbolic categories in language, have to be mapped on dynamic events in actions

(Bates et al., 1994; Childers & Tomasello, 2006; Golinkoff & Hirsh-Pasek, 2008). As soon as the mapping has taken place, one could argue that the linguistic symbol (i.e., the verb) is an additional characteristic of the overall action representation (Barsalou, 2008). Thus, the cognitive and the linguistic representations are intertwined. Because the processing of action representations through the MNS is potentially based on associative learning, it seems likely that the MNS is involved in action-verb processing as soon as an association is built between motor and sensory areas (Heyes, 2010). Research has shown that adults and children from preschool age on recruit their sensorimotor system during the processing of action verbs, in contrast to abstract verbs (Hauk, Johnsrude, & Pulvermüller, 2004; Hauk & Pulvermüller, 2011; K. H. James & Maouene, 2009; K. H. James & Swain, 2011; Moreno et al., 2013; Niccolai et al., 2014; Pulvermüller, 2005; Raposo, Moss, Stamatakis, & Tyler, 2009; Rueschemeyer, Brass, & Friederici, 2007; Tettamanti et al., 2005; Van Dam, Rueschemeyer, & Bekkering, 2010; van Elk, van Schie, Zwaan, & Bekkering, 2010). These studies have shown that abstract verbs recruit the MNS to a smaller extent than action verbs (Moreno et al., 2013; Repetto, Colombo, Cipresso, & Riva, 2013; Rueschemeyer et al., 2007; van Elk et al., 2010). This is in accordance with the assumption that stronger sensorimotor links, such as those for action verbs in contrast to abstract verbs, elicit higher MNS activity (Heyes, 2010). Furthermore, a study in adults has demonstrated that verbs which have not been linked to an action at all (i.e., pseudoverbs) do not trigger MNS activity (Fargier et al., 2012). However, a short associative training in which pseudoverbs get associated with observable actions results in sensorimotor involvement during processing of pseudoverbs in adults (Fargier et al., 2012). In sum, associative learning is a potential mechanism that enables the MNS to process action verbs. An important question is, however, which processes take place after the MNS has been enabled to process action verbs.

The direct-matching account suggests that the mechanism for action-verb processing is similar to processing observed actions (Barsalou, 2008). This idea proposes that action verbs get directly mapped onto the a motor program within the MNS of the listener, which in turn activates a fronto-parietal brain network, and meaning is derived from the heard action verb (Pulvermüller, 2005). This proposal raises, however, two problems, which make it an unlikely mechanism for the sensorimotor involvement during action-verb processing. First, automatic mapping of the action verb on a motor program in one's MNS would imply that it is mapped on sensorimotor functions used to produce the perceived stimulus because this is what was stated for observed actions (Rizzolatti & Craighero, 2007). Concretely, this would mean that a heard verb would be mapped onto articulatory motor programs (i.e., motor programs used to pronounce the verb; Glenberg & Gallese, 2012; Liberman, 1993; Rizzolatti & Craighero, 2007). However, such a mechanism is difficult to arrange with the often-reported somatotopic distribution of activity during action-verb processing (Buccino et al., 2005; Hauk et al., 2004; K. H. James & Maouene, 2009; Tettamanti et al., 2005). Specifically, it has been shown that hand-related action verbs (e.g., to pick) activate sensorimotor hand areas, whereas foot-related action verbs (e.g., to kick) activate sensorimotor foot areas (Hauk et al., 2004; K. H. James & Maouene, 2009; Pulvermüller, 2005; Tettamanti et al., 2005). If direct matching were the mechanism explaining how we process action verbs, this would mean that the motor programs for action execution and the motor programs for speech production are activated simultaneously.

Second, as in the case of action observation, direct matching has difficulties accounting for higher-level intentions (i.e., why is someone saying something, does he mean what he says?). Therefore, it is important to ask when and why we use verbs in order to get closer to a potential neural mechanism that underlies verb processing. We use verbs to describe events, processes, and relations, that is, things that happen to our environment or us (Golinkoff & Hirsh-Pasek, 2008). This means that we use verbs to share our experiences and mental states with others. When we share our experiences with others in a linguistic way, we draw on a common representation of the referent. Referring to an event is a linguistic way of directing the interaction partner's attention to the event (Tomasello, 2003). This suggests that language can be used to manipulate the mental states of our interaction partners, just as it was proposed for actions (Abramova, 2018; Tomasello, 2003). In a predictive coding framework, one could argue the MNS is the neural basis for the selection of the best possible way to understand and manipulate others' mental states (Keysers & Gazzola, 2014; Kilner, 2011; Kilner et al., 2007b), irrespective of the modality of the communicative signal. This suggests that the MNS uses predictive processing to interpret what a verb means (Fischer & Zwaan, 2008).

The predictive coding account proposes an initial temporal lobe processing of overall semantics generating predictions which are passed along the lower hierarchical levels of the MNS, leading to a confirmation or updating of initial semantic processing (Kilner, 2011). Pulvermüller (2017) argued that once an action-processing system, such as proposed by the predictive coding account (Kilner et al., 2007a), is in place, it is reused for the processing of language that is action-related. If this holds true, we have to presume that action representations in the medial temporal cortex do not only comprise activation patterns from visual input but also from auditory and linguistic input. Consequently, auditory and linguistic input should activate the general action representation, again resulting in a similar prediction process as explained for the visual input (Caramazza et al., 2014; Mahon & Caramazza, 2008). Therefore, hearing an action verb would involve semantic processing on the high level of the overall action representation. Predictions would be passed along the MNS confirm and update the initial semantic processing of the verb (Kilner, 2011). Note that the MNS comprises the sensorimotor areas, which would be involved in executing the action the verb refers to (Pineda, 2008). Neurorobotics confirms the idea that verb meaning is tightly linked to the movements one would perform to execute the action meant by the verb (Marocco, Cangelosi, Fischer, & Belpaeme, 2010).

An advantage of the predictive coding account is the ability to investigate higher-order features of communicative signals, such as intentions or other contextual features. This is of great importance because, similar as for the processing of observed actions, higher-order features, such as context, impact the activation of the MNS (Hickok, 2009; Keysers & Gazzola, 2014). This means that the embedding in a sentence but also the intention of communication could impact the activity of the MNS, measured by sensorimotor activity in most studies. In accordance with this, Fischer and Zwaan (2008) suggested that we use the MNS to derive predictions from the language input. If an action verb is embedded in a sentence, we can derive *communicative predictions* (Fischer & Zwaan, 2008). Communicative predictions are described as predictions about the continuation of the language input, based on parts of the language input (Fischer & Zwaan, 2008). Therefore, communicative predictions are predictions from language about language (Fischer & Zwaan, 2008). For example, we can complete a sentence, predicting the object based on the subject and the verb that are available. Behavioral studies show that with 24 months of age toddlers make communicative predictions, especially if they have a large expressive vocabulary available (Mani, Daum, & Huettig, 2016; Mani & Huettig, 2012). Neurophysiological research in adults has pointed out that the language context in which the action verbs occur has a great influence on whether the sensorimotor system, as a proxy for MNS activity, gets involved in processing or not (Lam, Bastiaansen, Dijkstra, & Rueschemeyer, 2016; Raposo et al., 2009; Tomasino, Weiss, & Fink, 2010). For instance, action verbs that occur in sentences with negations are associated with less sensorimotor activity than action verbs in non-negated sentences (Tomasino et al., 2010). Furthermore, it has been shown that idiomatic and metaphoric expressions (e.g., grasping an idea) are associated with less sensorimotor activity than literal sentence (e.g., grasping an apple), although they both comprise the same action verb, which would clearly elicit sensorimotor activity if presented in isolation, that is, out of the context of a sentence (Raposo et al., 2009). However, a further study showed that action verbs within idiomatic contexts are still more similar to literal sentences than to abstract sentences with abstract verbs (Schaller, Weiss, & Müller, 2017). To sum up, all these studies suggest that the involvement of the sensorimotor system is dependent on the semantics of the verb within its context, if available.

Importantly, there are not only different language contexts in which an action verb can occur but also different action contexts. This might impact the involvement of the MNS in processing the action verb and the actions, too. This is in line with Fischer and Zwaan's proposal (2008) stating that we make a second type of predictions based on the language input, namely *referential predictions*. Referential predictions are predictions from language about actions. More specifically, referential predictions take the language input as a basis to predict which action is going to follow next (Fischer & Zwaan, 2008). They are, so to say, important to determine why an interaction partner made a certain utterance, what this utterance means, and what consequences there are to this utterance (Fischer & Zwaan, 2008). Behavioral studies in adults showed that action prediction was facilitated following the presentation of a (dynamic) action verb, compared to a word which was not action-related (Springer et al., 2012; Springer & Prinz, 2010). In the light of Fischer and Zwaan's theory (2008), subjects potentially made referential predictions based on the action verb, which, in turn, facilitated the upcoming action prediction. Similar behavioral findings have been obtained in an eye-tracking study with toddlers. Gampe and Daum (2014) used predictive gaze shifts, which are a standard measure for action prediction, to study the impact of referential predictions on subsequent action prediction. Specifically, they tested whether referential predictions from action verbs facilitate action predictions for observed actions in infants and toddlers, depending on their expressive verb vocabulary. Results indicated that the action verb facilitated action prediction during subsequent action observation only for the group of 24-month-olds, compared to 12- and 18-month-olds. The authors assumed that the differences between the age groups stem from a difference in expressive vocabulary. This indicates that it might be referential predictions that can facilitate action prediction early in development, but only if toddlers are sufficiently skilled in expressive language (Gampe & Daum, 2014).

Fischer and Zwaan (2008) proposed that the MNS, especially the sensorimotor system, is involved in making referential predictions. Furthermore it has been suggested that enhanced activity of the sensorimotor system underlies facilitated action prediction (Springer et al., 2012; Springer & Prinz, 2010), which would mean that the action verb affected the sensorimotor activity needed for subsequent action prediction. However, Springer and colleagues (2012) and Springer and Prinz (2010) can only speculate on the influence of action verbs onto the sensorimotor system in terms of a priming effect because they did not directly assess sensorimotor activity. Nevertheless, there is some evidence that action verbs do indeed exhibit priming effects of sensorimotor cortices: Klepp, Niccolai, Buccino, Schnitzler, and Biermann-Ruben (2015) demonstrated that action verbs can enhance sensorimotor activity during action execution. This study indicates that action verbs can prime motor programs. From an MNS perspective, assuming a strong link between action execution and action observation, similar priming could be possible for action verbs onto action observation. Importantly, such priming effects do not yet demonstrate that action verbs trigger referential predictions that influence subsequent action prediction. However, Elsner and colleagues (2013) found that predictive gaze shifts, which are a standard eye-tracking measure for action prediction and which were used in Gampe and Daum (2014), are causally related to the activity of the motor system in adults. Therefore, this study links the behavioral findings from eye tracking to studies investigating the MNS, showing that action prediction assessed by behavioral measures are the product of enhanced sensorimotor activity. Taken together, these findings suggest that action verbs have an impact on action prediction, which can be measured on a behavioral and a neural level (especially the MNS).

1.6. Research questions

In the previous chapters, I discussed theoretical perspectives and empirical evidence suggesting that action and language, as domains of communicative signals, are interrelated. The interrelation concerned the existence of a common processing system (i.e., the MNS), a common processing mechanism (i.e., predictive coding), and cross-domains influences on processing (i.e., action verbs facilitate action prediction).

Research has provided evidence for the involvement of the MNS in action processing from infancy to adulthood (Fox et al., 2016; Marshall & Meltzoff, 2011). In contrast, developmental studies are still rare in the language domain, and it is still unclear when the MNS starts being involved in action-verb processing. Studies in adults and preschoolers suggest that action verbs are processed in a similar way as observed actions (K. H. James & Maouene, 2009; Moreno et al., 2013). They seem to share a common basis. Such a common basis on a representational level is highly plausible because action verbs are tightly linked to perceived actions. Furthermore, Golinkoff and Hirsh-Pasek (2008) suggest that verb acquisition is based on mapping linguistic symbols (i.e., action verbs) onto cognitive representations of actions. As a result action verbs become part of the overall action representation (Barsalou, 2008; Golinkoff & Hirsh-Pasek, 2008). Assuming that the MNS takes part in processing communicative signals using action representations (Kilner, 2011), one would argue that the MNS is involved in action-verb processing as soon as an action verb has been acquired. Therefore, the current dissertation project investigated the question whether the MNS of toddlers, who are at the beginning of verb acquisition, is involved in processing action verbs similar to processing actions. It was assumed that, at this age, action verbs should to some extent be associated with existing representations of familiar goal-directed actions (Fischer & Zwaan, 2008) because they have been mapped onto actions that are already represented during verb acquisition (Bates & Dick, 2002; Gentner & Boroditsky, 2001; Golinkoff & Hirsh-Pasek, 2008). Consequently, it was expected that toddlers' MNS is involved in action-verb processing.

Under the premise that the MNS is already involved in action-verb and action processing in toddlerhood, the question about the underlying mechanism comes up. In the action domain, direct matching (Rizzolatti et al., 2001) but also predictive coding (Kilner, 2011; Kilner et al., 2007a) have been discussed as potential candidates. Predictive coding has the advantage that it can account for contextual effects as well as effects of expertise (Keysers & Gazzola, 2014; Kilner, 2011). Furthermore, the predictive coding account sees the processing of an action representation as starting point of comprehending and interpreting observed actions (Kilner, 2011; Kilner et al., 2007a). According to embodied cognition, action representations comprise different modalities, and language is one of them (Barsalou, 2008). This means that action-related language, such as action verbs, could trigger predictive processes as well. Behavioral studies in adults but also in toddlers indicate indeed that action verbs might elicit predictive processes (i.e., referential predictions; Fischer & Zwaan, 2008) which affect upcoming action prediction (Gampe & Daum, 2014; Springer et al., 2012; Springer & Prinz, 2010). However, the neural underpinnings of this effect are still not clarified. Therefore, the current dissertation project investigated whether the MNS of toddlers is involved in predictive processing for action verbs, which in turn affects action prediction.

Investigating the question whether action verbs impact action predictions within the MNS addresses the question of the importance of context for action processing, which is an inherent part of predictive coding (Kilner, 2011). In the case of action verbs that are presented with the observed action, the context information is not visual but linguistic (i.e., the action verb sets the stage for what will be observable). However, the experience one has with the processing of communicative signals (i.e., actions and language) is another important factor to address when studying action processing in the context of action language. For instance, the MNS is more involved in the processing of observed actions for which the observer has much experience than in the processing of actions for which the observer has less experience (Calvo-Merino et al., 2005; Cannon et al., 2014; Liew et al., 2013; van Elk et al., 2008; Yoo et al., 2016). It is assumed that high experience with performing an action is associated with more pronounced MNS processing because of the increased connectivity between sensory and motor brain areas (Cooper et al., 2013; Heyes, 2010; Pulvermüller, 2017). Furthermore, a strong link between sensory and motor areas is also beneficial for efficient predictive processing because it strongly weights the most probable sensory program, based on a certain motor program (Keysers & Gazzola, 2014). Such an effect of experience might translate from the action domain to the language domain. At the beginning of verb acquisition, at around 18 months of age, action verbs are foremost part of the receptive vocabulary of toddlers. At 24 months of age, toddlers have expressive experience with the verbs (Bates et al., 1994). Thus, only the 24-month-olds have substantial experience in uttering the action verb. Behavioral evidence corroborates the assumption that action-verb processing differs depending on the expressive vocabulary of the toddlers (Gampe & Daum, 2014). Therefore, the current dissertation project investigated whether toddlers who differ in expressive experience for action verbs (i.e., 18-month-olds and 24-month-olds) vary in the way they involve their MNS in the processing of action verbs. On the one hand, studies suggest that expressive verb repertoire might have a beneficial effect on verb processing because experience in pronouncing the verb is associated with richer representations of the latter (Munakata, 2001; Shinskey & Munakata, 2005). On the other hand, studies argue that first-hand experience with performing actions is beneficial for acquiring and processing verbs (Gampe, Brauer, & Daum, 2016; K. H. James & Swain, 2011). It remains to be clarified which of the two possibilities is more plausible.

Taken together, this dissertation project investigated three main questions: 1) Is the MNS of toddlers, who are at the beginning of verb acquisition, involved in processing action verbs similar to processing actions? 2) Is the MNS of toddlers involved in predictive processing for action verbs, which in turn affects action prediction? 3) Do toddlers who differ in expressive experience for action verbs (i.e., 18-month-olds and 24-month-olds) vary in the way they involve their MNS in the processing of action verbs?

In order to answer these questions, I conducted two studies in 18- and 24-month-olds applying EEG to measure the activity of the MNS. EEG is the most convenient method to assess the activity of the MNS across development because it is non-invasive, applicable even in infants, and has high temporal resolution (Cuevas, Cannon, Yoo, & Fox, 2014; Fox et al., 2016; Marshall & Meltzoff, 2011). Measuring the activity of the MNS is achieved by assessing two types of brain oscillations which can be found over sensorimotor sites, thus in the extended MNS: the mu rhythm (8-13 Hz), which is an alpha rhythm, and its harmonic rhythm, the beta rhythm (15-30 Hz; Fox et al., 2016; Hobson & Bishop, 2016; Palmer, Zapparoli, & Kilner, 2016). It has been shown that the mu rhythm originates from somatosensory cortices, whereas the beta rhythm has its source in the primary motor cortices (Caetano, Jousmäki, & Hari, 2007; Gerloff et al., 2006; Hari et al., 1998; Pfurtscheller & Lopes da Silva, 1999). Both oscillations display high power (i.e., squared amplitude), when the sensorimotor system is at rest, thus in an idling state (Pfurtscheller, 2001; Pfurtscheller & Lopes da Silva, 1999). The high power is a result of large neuron populations that fire in synchrony (Pfurtscheller & Lopes da Silva, 1999). If the sensorimotor system is activated, post-synaptic responses in pyramidal cells are induced, which lead to a desynchronization of the neuronal population and consequently to a desynchronization of the mu and beta rhythms (Pfurtscheller & Lopes da Silva, 1999). The desynchronization of a neural oscillation, also called suppression, describes a decrease in power due to a stimulus, in comparison to a pre-stimulus reference period (Pfurtscheller, 2001; Pfurtscheller & Lopes da Silva, 1999). This means that we can measure if the MNS of toddlers responds to action verbs and observed action by observing if sensorimotor oscillations get suppressed. Of the two sensorimotor oscillations, I focused on the mu rhythm because most studies in infants and toddlers investigated this frequency band (Fox et al., 2016; Lepage & Théoret, 2006; Marshall & Meltzoff, 2011). Furthermore, it has been demonstrated that the mu rhythm is functionally and topographically similar from infancy to adulthood, although the frequency range is overall lower in infants and increases across development until it reaches the adult frequency range (Cuevas et al., 2014; Fox et al., 2016; Marshall & Meltzoff, 2011). Functional similarity refers to the suppression of the mu rhythm in response to an action that is performed and an action that is observed (Cuevas et al., 2014; Fox et al., 2016). Topographic similarity, instead, refers to the presence of the suppression over central sites of the scalp in all age groups (Cuevas et al., 2014; Hobson & Bishop, 2016). However, in infants and toddlers the topography is often less focused, which means that mu suppression is also measureable at parietal and, in rare cases, also at occipital sites (Fox et al., 2016).

2. Studies

In the following two paragraphs, I will specify the research questions that guided the experiment. Furthermore, I will highlight the design and results of the two studies conducted in this dissertation project. For each study the full and more detailed description can be found in Part II of this thesis in which the empirical articles are documented.

2.1. Study 1

The aim of this study was to answer the question whether the sensorimotor system of toddlers, who are at the beginning of verb acquisition, is involved in processing action verbs, similar to processing observed actions. This question was based on embodied cognition stating that every external stimulus which is related to an action is processed by the MNS (Barsalou, 2008). In addition, it has been suggested that such a relation between actions and language is the cornerstone of verb acquisition, which is a process in which words get mapped onto actions (Gentner & Boroditsky, 2001; Golinkoff & Hirsh-Pasek, 2008). Therefore, we assumed that a toddler's MNS should be involved in action and language processing as soon as a verb has been acquired (i.e., as soon as the verb has been mapped onto an action). Furthermore, the study aimed to scrutinize the role of experience with action verbs (i.e., status of verb acquisition) for sensorimotor processing action verb in detail.

To this end, 18- and 24-month-olds ($N = 47$) were presented with auditory action verbs and pseudoverbs while the sensorimotor response to the stimuli was measured by means of EEG assessing the suppression of the mu rhythm at three different electrode sites (left/right central, occipital). Pseudoverbs were used to contrast action verbs because it has been shown that pseudoverbs are not associated with sensorimotor activity although their morphology is verb-like (Fargier et al., 2012). Thus, pseudoverbs are an ideal contrast to action verbs because they differ only in terms of semantics but not morphology. In addition to the presentation of action verbs and pseudoverbs, the toddlers observed video clips of the corresponding means-end actions in the second half of the paradigm. The two age groups were chosen to operationalize the experience with action verbs because 24-month-olds already have a substantial expressive verb vocabulary, while 18-month-olds represent action verbs predominantly in their receptive vocabulary.

Results indicated that mu suppression differed between action verbs and pseudoverbs only at left central electrode sites ($t(46) = -2.10$, $p = .042$). Further analyses indicated that only action verbs but not pseudoverbs were associated with mu suppression within left central electrode sites ($t(46) = -2.24$, $p = .030$). Moreover, observed actions were associated with mu suppression as well. Here, we only analyzed toddlers who had enough artifact-free trials (minimum 6 trials per condition) for both action-verb presentation and action observation ($n = 33$). The sensorimotor activity for observed action was present at right central ($t(32) = -10.6$, $p < .001$) and occipital electrode sites ($t(32) = -4.31$, $p < .001$). Furthermore, analyses on the effect of experience indicated that the two age groups did not differ with respect to sensorimotor activity in response to either action verbs or observed actions (all $p > .073$).

We interpret the results in such a way that action verbs are associated with sensorimotor activity because they are part of an overall action representation comprising different modalities (e.g., observational, auditory, linguistic). This was not the case for pseudoverbs because they were completely novel, and they have never been associated with an action. Furthermore, the similarity in the processing of action verbs and observed actions points to a common processing system for different communicative signals.

2.2. Study 2

The aim of this study was to investigate the role of action verbs in the action prediction process. More specifically, the study investigated if referential predictions from action verbs facilitate action predictions. This was based on behavioral findings from adult and toddler studies demonstrating that action verbs facilitate subsequent action prediction of corresponding actions (Gampe & Daum, 2014; Springer et al., 2012; Springer & Prinz, 2010). Furthermore, it has been suggested that action verbs and observed actions are part of an overall action representation (Barsalou, 2008), which is used for processing different communicative signals. This processing is assumed to be characterized by predictions and prediction errors generated by comparing the predictions against sensory evidence (Kilner et al., 2007a). On the highest level of such a predictive process stands the action representation (Kilner, 2011). It has been assumed that language, which is part of the action representation, can prime the neural system for the processing of an observed action by referential predictions, which are predictions derived from language input about what is going to happen next (Fischer & Zwaan, 2008). Furthermore, it has been suggested that experience with action-related language impacts the facilitating effect on action prediction (Gampe & Daum, 2014). Therefore, the current study also investigated this effect of experience on the neural facilitation of action prediction through action verbs.

We presented 24-month-olds (*N* = 32) with sentences either comprising an action verb (e.g., I'll show you cutting) or a neutral linguistic expression (e.g., I'll show you something). After each sentence the toddlers observed a corresponding means-end action in a video clip. To assess action prediction, we recorded EEG to measure the suppression of the mu rhythm as indicator for sensorimotor activity at three electrode sites (left/right centro-parietal, occipital).

Results for the group of toddlers with high expressive experience with the action verb (n = 17) showed that the left sensorimotor system was more active during verb presentation than during the presentation of the neutral linguistic expression ($\chi^2(N = 17) = 1392.72$, $p < .001$). Furthermore, left-lateralized sensorimotor activity during action observation was increased after having listened to a sentence with an action verb, compared to a sentence with a neutral linguistic expression ($\chi^2(N = 17) = 2172.81$, $p < .001$). These results were not confirmed for the group of toddlers with less expressive experience with action verbs (n = 15, all $p \geq .239$).

We argue that the results regarding verb processing speak for experience-dependent referential predictions derived from the action verbs. Furthermore, we interpret the findings in such a way that action verbs facilitated subsequent action prediction during action observation, in toddlers who have the action verbs in their expressive vocabulary. Our study suggests that language and action are interrelated because they share the MNS as common processing system and processing mechanism, namely predictive coding, and because language processing impacts action processing.

4. General discussion

In the following sections, I will discuss Studies 1 and 2 in the broader scope of empirical evidence and theoretical considerations. The first section is dedicated to the involvement of the MNS in language processing early in language development. I will discuss how the findings of Studies 1 and 2 provide evidence for such an early involvement of the MNS in language processing. The second section discusses the possible function of this involvement of the MNS in the processing of language. I will consider a direct-matching perspective as well as the predictive coding account in order to make a point in favor of predictive processing. In the third section, I will highlight what the current studies can contribute to the debate about the development of mirroring properties, focusing on associative learning and a neuroconstructivist perspective of overall development. To conclude, I will highlight the limitations of Study 1 and 2 and propose a new approach for future research.

4.1. The mirror neuron system and early language processing

The first research question of this dissertation project was whether the MNS of toddlers, who are at the beginning of verb acquisition, is involved in processing action verbs similar to processing actions. Study 1 demonstrated that toddlers of 18 and 24 months of age involve their sensorimotor system for the processing of observed goal-directed actions as well as action verbs but not pseudoverbs. Further, Study 2 corroborated Study 1 by showing that action verbs but not neutral linguistic expressions are associated with sensorimotor activity. The sensorimotor system is a part of the extended MNS in humans (Pineda, 2008). Therefore, Studies 1 and 2 show that the MNS of toddlers is involved in processing diverse action-related input from the action and the language domain. This is in line with theories on embodiment, which argue that everything, that is, perception, language, emotion, and cognition, is grounded in motor programs and interoception (Barsalou, 2008; W. James, 1890). The discovery of the MNS in monkeys and in humans has corroborated the assumption that, at least, action perception and action production have something in common, namely a neural processing system. To date, there is a vast amount of research, from infancy to adulthood, additional to Study 1, demonstrating that the MNS is involved in processing observed actions (for a review see Fox et al., 2016). In line with embodied cognition, studies in adults and children, as well as Studies 1 and 2 demonstrated that action verbs are associated with sensorimotor activity (Hauk et al., 2004; K. H. James & Maouene, 2009; Niccolai et al., 2014; Pulvermüller, 2005; Repetto et al., 2013; Rueschemeyer et al., 2007). Studies 1 and 2 are especially interesting because they show a very early involvement of the MNS in action-verb processing, namely at a point in development in which action verbs begin to be acquired (Bates & Dick, 2002; Golinkoff & Hirsh-Pasek, 2008). Study 1 showed that, even if the action verbs are only part of the receptive vocabulary, the MNS is already involved in processing the action verbs. Therefore, the current studies demonstrate that a common neural system is endowed with the ability to process observed actions and action verbs, which are regarded as parts of an overall action representation (Barsalou, 2008). The similarities in processing are quite evident, but there are also differences, especially with respect to lateralization.

In Studies 1 and 2, the sensorimotor activity during the processing of an action verb was lateralized towards the left-hemisphere, while the processing of observed actions was not. This might suggest that sensorimotor action-verb processing has fundamental similarities with general language processing, which takes place in the left hemisphere as well (Knecht et al., 2000). Furthermore, the left-dominant sensorimotor processing of action verbs makes sense in the light of a strong interconnection of the inferior frontal gyrus, including Broca's area, which is associated with language functions, and the inferior parietal lobule (Keysers & Gazzola, 2014; Pineda, 2008). The sensorimotor cortices are an interface between inferior frontal and parietal areas, which means that they translate motor to sensory signals (Johnson

& de Haan, 2015). Furthermore, the sensorimotor cortices seem to be active whenever the inferior frontal gyrus is involved in mirroring (Pineda, 2008). This is in line with the assumption that sensorimotor action-verb processing parallels with general language processing because Studies 1 and 2 both found left-lateralized sensorimotor processing for action verbs. However, the link between inferior frontal activity and sensorimotor activity is likely not as automatic as proposed by Pineda (2008) because Studies 1 and 2 did not reveal any sensorimotor activity for pseudoverbs and neutral linguistic expressions. The pseudoverbs and the neutral expressions are also language stimuli, which should be processed by the inferior frontal gyrus. This implies that there is more to the sensorimotor activity associated specifically with action verbs than mere language processing. The finding that action verbs but not the other language stimuli involved the MNS in processing might suggest that the MNS processes meaning. And because observed actions and action verbs are communicative signals it remains to be clarified what function the MNS in processing of meaning has.

4.2. Processing communicative signals

The second question of this dissertation project was whether the MNS of toddlers is involved in predictive processing for action verbs, which in turn affects action prediction. In this chapter, I will discuss Study 1 and Study 2 with respect to the evidence for predictive coding during action-verb processing. Subsequently, I will focus on Study 2 and predictive processes, foremost referential predictions, taking place when action verb and actions co-occur.

The function of the MNS in action processing but also in language processing is highly debated. At first glance, the results of Study 1 seem to be in favor of the direct-matching account, which proposes that perceived stimuli get automatically mapped onto the corresponding motor programs, and by means of this process the stimulus is understood, thus meaning is derived (Rizzolatti et al., 2001). Study 1 seems to be in favor of this because observed actions and action verbs automatically activate the sensorimotor system of the toddlers but pseudoverbs don't. Even Study 2 could provide evidence for direct matching if we consider the MNS activity for action verbs regardless of the subsequently observed action. A number of studies in adults favor an interpretation according to the direct-matching account because they show a very fast, automatic sensorimotor response to action verbs, suggesting that the system derives meaning and does not process meaning that has been derived elsewhere, which would provoke more delayed responses (Boulenger, Shtyrov, & Pulvermüller, 2012; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Shtyrov, Butorina, Nikolaeva, & Stroganova, 2014; Vanhoutte et al., 2015).

However, there are at least two issues that need further attention before an interpretation of Study 1 and 2 according to direct-matching can be declared valid: First, other studies in adults indicate activity of the MNS during action-verb processing at a later stage making a claim for semantic re-analysis (Papeo, Vallesi, Isaja, & Rumiati, 2009; van Elk et al., 2010). Second, it is still an open question for the language domain, what motor programs are matched with the sensory input, that is, an action verb. This is an important point with respect to the discussion if meaning is derived or re-analyzed by the sensorimotor system. The direct-matching hypothesis would assume that a stimulus is mapped onto a corresponding motor program, that is, if we see a grasping hand, we map it onto our grasping motor program (Rizzolatti et al., 2001). If instead, we hear someone saying "grasping", we would map it onto our motor program for saying "grasping" (Rizzolatti & Craighero, 2007). According to the direct-matching account, the MNS will derive meaning from the articulatory motor program, analogous to the way meaning is derived for observed actions (see Fig. 1).

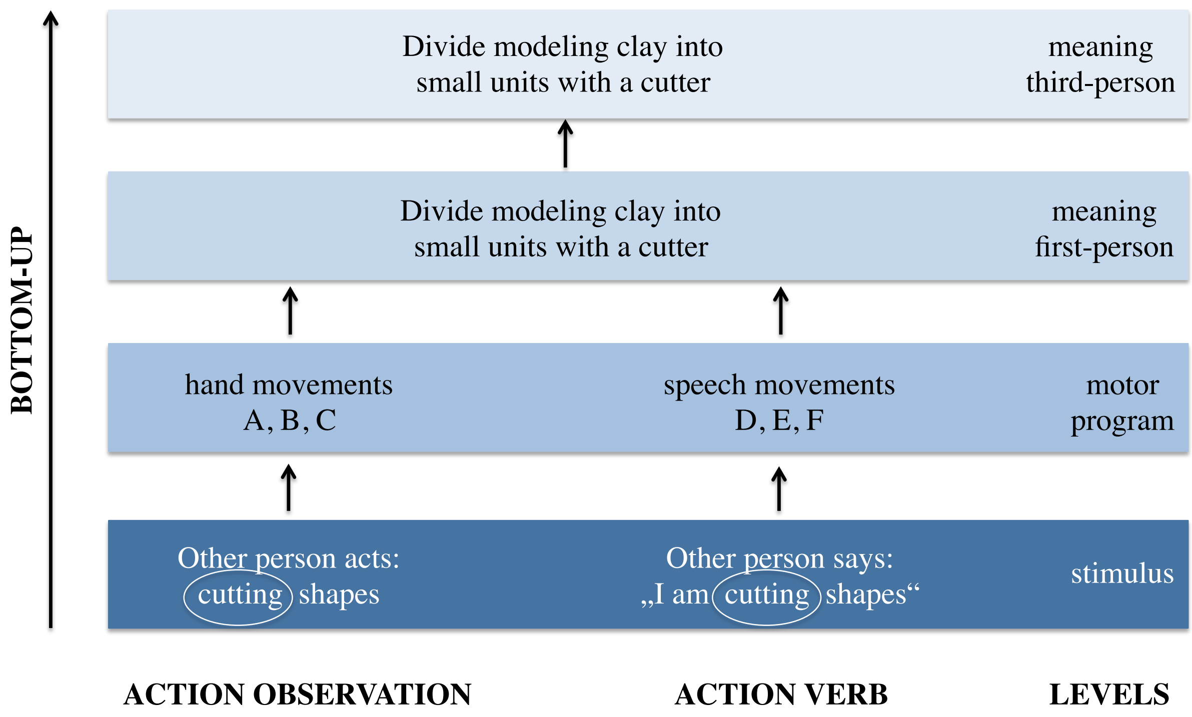

Fig. 1. Flow chart illustrating how meaning is derived according to the direct-matching account.

The process of deriving meaning is conceptualized as bottom-up process starting at the stimulus level, leading to an understanding from a third-person perspective. The stimulus level comprises everything that an observer can hear or see, which related to the action. The level of the motor program describes the motor programs that the observer would need to perform the observed action or utter the action verb. The meaning on a first-person level indicates what an action or an action verb means in the eyes of the observer, while the third-person level indicates why the actor has performed the action or uttered the action verb.

With respect to Fig. 1, the direct-matching account would claim that the inferior frontal gyrus is involved in the processing on the level of the motor program (Rizzolatti et al., 2001) and the sensorimotor cortex at the interface between the motor program and the meaning on first-person level (Johnson & de Haan, 2015). If this holds true, pseudoverbs are not associated with sensorimotor activity because there is no meaning on the first-person level that can be constructed although the pseudoverb per se is probably processed by the inferior frontal gyrus. This is in line with research in adults, which demonstrated that the sensorimotor system is not active when processing meaningless syllables (Crawcour, Bowers, Harkrider, & Saltuklaroglu, 2009). For the neutral linguistic expression from Study 2, a similar process might take place, but instead of no meaning only a very vague representation can be derived, which results in less sensorimotor activity for neutral linguistic expressions than for action verbs. So far, the direct-matching approach seems to be suitable to describe the findings from the current two studies. However, it is also possible that the role of the sensorimotor system in deriving meaning from perceived stimuli is less automatic and exclusive (Csibra, 2007; Kilner, 2011; Kilner et al., 2007a) because a fundamental problem of the direct-matching account is that the meaning on the first-person level and the meaning on the third-person level are automatically equal, not accounting for the vast amount of meanings a communicative signal can have (Caramazza et al., 2014; Hickok, 2009). For instance, one can grasp a cutter to cut shapes for modeling clay, or to use it as pattern to draw shapes, or even to throw it on the floor in the case of frustration. In these three examples, grasping the cutter means three different things. Equally, an utterance can have several meanings. Therefore, to describe processing of communicative signals, it is important to have a mechanism at hand that can deal with context, multiple meanings, and intentions, which are potentially not equally probable.

Predictive coding describes such a mechanism that can deal with multiple higher-order intentions and goals (Kilner, 2011; Kilner et al., 2007a). Therefore, it offers a more flexible way, compared to direct matching, to investigate how the MNS contributes to the processing of communicative signals, such as actions and sentences comprising action verbs. Predictive coding assumes that we predict communicative signals from previous communicative signals and test the most probable prediction against what we actually perceive (Kilner et al., 2007b). This is interesting because it implies that we can predict from action verbs what kind of actions will follow (Fischer & Zwaan, 2008). Study 2 tested this assumption and found that predictions derived from action verbs facilitate subsequent predictions in an observed action, measured by increased activity of the sensorimotor system, compared to a neutral expression. This is in line with behavioral studies from adults and toddlers, which used a similar paradigm (Gampe & Daum, 2014; Springer et al., 2012; Springer & Prinz, 2010). From a predictive coding perspective, Study 2 provides evidence for predictions derived from action verbs: the sensorimotor system was active during action-verb processing, which is a sign of a referential prediction (Fischer & Zwaan, 2008), and this activity enhanced subsequent sensorimotor activity in the process of action prediction, which is a sign for faster action prediction (Elsner et al., 2013). Already in Study 1, there was sensorimotor activity related to action-verb processing, which can be interpreted as an indicator for a referential prediction. However, Study 1 cannot test whether toddlers have predicted what will happen next because the design of the study did not foresee that anything would happen after the verb presentation. Moreover, there was no additional evidence whatsoever that the toddlers could have used to verify by means of predictions and prediction errors that their understanding of the action verb is correct (or at least good enough). This is clearly an advantage of Study 2, compared to Study 1, because toddlers were provided with the visual information of what is going to happen next. This allowed quantifying the effect of referential predictions on the actual prediction of what is happening. If the sentences comprising action verbs were only associated with communicative predictions, we would not have expected an effect on subsequent action prediction during action observation. This is because communicative predictions act within the language domain, while referential predictions act across domains; from language onto action (Fischer & Zwaan, 2008). Therefore, Study 2 demonstrates an effect of referential predictions on later action predictions because both predictions construe models in the action domain (i.e., what will happen next, based on what I heard/saw before?). Importantly, for predictive coding, it is not relevant if the initial prediction comes from the action domain or the language domain because the initial prediction is made from a higher-level multimodal representation, as in the case of Study 2 (Barsalou, 2008). This also suggests that cognition, action perception, and language are not parallel and unrelated (Chomsky, 2009) but rather interrelated domains that impact each other during processing (Barsalou, 2008; Bruner, 1964; Mandler, 1988).

An issue that comes up with respect to the interpretation according to predictive coding is related to multisensory integration. Multisensory integration describes the simultaneous processing of stimuli from different sensory modalities. It is assumed that stimuli from different sensory modalities share modality-independent features, which is called *intersensory redundancy* (Bahrick, 2010). The intersensory redundancy hypothesis suggests that these modality-independent features are highly salient, and therefore, multimodal stimulation will be associated with increased neural activity compared to unimodal stimulation (Bahrick, 2010). Applied to Study 2, this could imply that action verbs and observed actions trigger mental codes of different modalities within an overarching representation of an action. This means that the toddlers might have rather experienced multimodal stimulation when hearing an action verb followed by an observable action than having made predictions. This is because they were presented with a linguistic and an observation-based code of the action representation. To a lesser extent, this was also the case if they were presented with the neutral linguistic expression, because they were also provided with an observation-based code and a linguistic code of the action representation, but the linguistic code was not specifically tailored to a particular action. However, the design of the paradigm makes an interpretation of the MNS as a purely intersensory system unlikely because the codes from different modalities were presented sequentially and not simultaneously, as it is done in studies investigating multisensory integration (Bahrick, 2010). Furthermore, studies using simultaneous processing of action verbs and observed actions demonstrated that action verbs reduced adults' reaction times, adults' readiness potentials, and hindered action prediction during action observation in adults and infants (Boulenger et al., 2008; de Vega, Moreno, & Castillo, 2011; Klepp et al., 2015; Mirabella, Iaconelli, Spadacenta, Federico, & Gallese, 2012; Pomiechowska & Csibra, 2017; Sciutti, Lohan, Gredebäck, Koch, & Rohlfing, 2016), which is contrary to the findings from Study 2 as well as the behavioral evidence from Gampe and Daum (2014). Therefore, if stimuli are presented in a sequential manner, the predictive coding account describes the role of the MNS much more accurately than multisensory integration, which is: the action verbs provide a context in which predictions of observed actions are much quicker than without context (Lupyan & Clark, 2015).

However, the predictive coding account would suggest that these higher-order context features are not processed within the MNS, as suggested by the results of Study 2, but outside, namely in the medial temporal gyrus (Kilner, 2011; Kilner & Frith, 2008). According to this view, the MNS is involved in making lower-level predictions and in adjusting predictions based on available information (Kilner, 2011). However, this claim is based on the premise that the MNS is restricted to the core areas (inferior frontal gyrus, inferior parietal lobule, and superior temporal sulcus). Importantly, it is questionable to divide the medial temporal gyrus from the MNS because neurons with mirroring properties have been found in temporal areas of the human brain (Mukamel et al., 2010). This raises the possibility that the medial temporal gyrus is, in fact, part of an extended MNS (Pineda, 2008). Therefore, the claim that the MNS is not necessary for processing communicative signals depends very much on how broad the MNS is defined (i.e., only core MNS or also extended MNS) and what one intends with understanding. With understanding one can intend the retrieval of goals and intentions (Rizzolatti et al., 2001), but understanding can also be the entire process of retrieving a representation, confronting it with available evidence, and (if necessary) updating it (Keysers & Gazzola, 2014). The extended MNS is involved in such a process of confronting and updating (Kilner, 2011). Therefore, Study 2, investigating context-dependent action processing in the broadest sense, provides a solid basis to claim that the extended MNS is necessary for understanding.

However, it is correct to state that, to date, it is unclear on which level the MNS handles predictions from action representations in order to check the internal model against evidence (Kilner, 2011). Is it on a holistic level (i.e., how, why, and on what an action is performed; exact meaning of the action) or on a somatotopic level (i.e., how an action is performed; specifying the effector limb such as the hand used to execute the action)? In Study 1, we suggested that the MNS handles the semantics of an action verb because pseudoverbs were not associated with MNS activity. Study 2 corroborated this assumption showing that action verbs are associated with more sensorimotor activity than neutral linguistic expressions. However, we cannot specify if these semantics are holistic of somatotopic. Both assumptions are viable, and the current studies cannot speak in favor of one of them. This is clearly a limitation, which future studies should deal with. A further project, which is in preparation, is working on solving the question by implementing a condition in which the action verb and the subsequently observed action were incongruent with respect to the meaning of the action, but congruent with respect to the effector limb (Antognini & Daum, 2018). Preliminary results seem to indicate that action-verb congruency was not associated with differences in sensorimotor activity in the action-prediction phase. However, this was only true for half of the participants, who did, as expected, not show differences between the conditions before the action could be observed. Unexpectedly, the other half of participants did show differences in verb processing before the action was observed, which is very difficult to interpret. Therefore, these preliminary results need to be taken with caution because there were problems regarding the manipulation for half of the group (Antognini & Daum, 2018).

In sum, Studies 1 and 2 provide evidence for the assumption that the MNS serves making predictions and updating predictions in order to process action verbs. Furthermore, action verbs and observed actions do not seem to belong to completely distinct domains but are potentially part of an overall action representation, which is composed by action-relevant codes from various modalities. These codes are processed by means of predictions and updating functions of the extended MNS (Kilner, 2011; Pineda, 2008), already early in development.

4.3. Developing predictive functions

The third question of this dissertation project was whether toddlers who differ in expressive experience for action verbs vary in the way they involve their MNS in the processing of action verbs. I will discuss this question in the light of the results of Study 1 and 2 with a focus on developing predictive functions through associative learning.

It is oftentimes claimed that the MNS can process and interpret actions, as suggested by predictive coding, because of associative learning that has taken place beforehand (Press et al., 2011). I propose that Study 1 and Study 2 can extend this argument to the language domain and make a more general point: the MNS processes communicative signals after associative learning has taken place. In Study 1, the MNS was only involved in processing action verbs, which map onto a familiar action. This was not the case for pseudoverbs, which have not undergone associative learning, in contrast to action verbs that the toddlers encounter in everyday life (Golinkoff & Hirsh-Pasek, 2008). Furthermore, Study 1 provides evidence for associative learning because action verbs and observed actions, which map on each other, are processed in a similar way, which stands in contrast to pseudoverbs. This result is in line with a study in adults, which showed that participants processed action verbs and the corresponding actions similarly (Moreno et al., 2013). Moreover, a different study in adults demonstrated that associative learning is a valid mechanism for linking verbs and actions (Fargier et al., 2012). Therefore, MNS activity during the processing of action verbs and observed actions might be an indicator for the existence of an overall action representation based on codes from various modalities (i.e., visual, auditory, motor), which all involve processing in the MNS as proposed by the embodied cognition account (Barsalou, 2008).

An even stronger claim in favor of the associative learning account as basis for predictive coding is that the MNS activity differs with respect to the experience with an action verb. Study 2, but not Study 1, shows that referential predictions are only made by toddlers who had the action verbs in their expressive vocabulary. More specifically, only this group of toddlers showed a difference in MNS activity between the action verbs and the neutral linguistic expressions, while toddlers of the same age but with less experience with the action verbs did not show this difference in MNS activity. In Study 1, toddlers were grouped by chronological age instead of vocabulary. Therefore, results form Study 2 might more accurately reflect the effect of experience with the action verb. Moreover, in Study 2, the experienced children displayed facilitated action prediction subsequent to the referential predictions while the other group did not. These results are interpreted as an effect of associative learning. It is assumed that children who have the action verbs in their expressive vocabulary have more experience with the verb than the other group of children. More experience translates into more opportunity for associative learning and richer representations after associative learning (Munakata, 2001; Shinskey & Munakata, 2005). If children are more experienced or more familiar with the action verbs, the sensorimotor predictions might become better, reflected by more sensorimotor activity, as shown in Study 2. This is in line with many studies in adults and infants, which show enhanced sensorimotor activity in response to actions which the adults or infants are experienced with (Calvo-Merino et al., 2006; Cannon et al., 2014; Liew et al., 2013; van Elk et al., 2008; Yoo et al., 2016). Importantly, this is not only valid for observed actions but also for action-related sounds that have been linked to actions by training (Gerson, Bekkering, & Hunnius, 2015). I propose that infants and toddlers, who are experienced with the action verbs, have more instances of hearing and pronouncing an action verb at hand that they can use to build the initial model of what is going to happen after having heard an action verb. Such an experience-dependency of processing is in line with the predictive coding account, and it agrees with how development, in general, is conceptualized in recent years (Karmiloff-Smith, 2017; Westermann et al., 2007). However, it cannot be not excluded that the experience with the action, and not with the action verb, is the decisive factor. That is, toddlers who have more experience with a certain action might be advantaged in associating action verbs with these actions. This argument is based on the assumption that toddlers need to have a detailed cognitive representation of the action and its different characteristics (e.g., manner/path, source/goal) in order to map the action verb onto an existing action representation (Golinkoff & Hirsh-Pasek, 2008). Similarly, it has been suggested that more experience with an object is associated with a richer representation of the object label in children (Inkster, Wellsby, Lloyd, & Pexman, 2016). Furthermore, evidence shows that children who have had the chance to perform an action are better at learning the corresponding verb (Gampe et al., 2016).

To sum up, experiencing the social world around us provides us with opportunities to learn and to incorporate what we have learned into a bigger context. According to predictive coding this bigger context comprises a complex model building and hypothesis testing system, which is constantly updated (Kilner et al., 2007a). This idea is in line with neuroconstructivism, which states that development happens in a context of constraints between various levels (e.g., genes, brain anatomy, neural function, body function, environmental factors; Westermann et al., 2007). In my view, Study 2 suggests that associative learning is a valid mechanism to explain how changes of constraints happen, which will, in turn, affect a whole processing system. Initially, the increasingly rich cognitive representation of actions changes neural learning constraints that enable verb acquisition. This means that the neural system is only ready to acquire action verbs after the actions themselves are sufficiently well represented (i.e., how, why and on what object an action is performed). This is in line with Bruner's (1964) conceptualization of cognition and language development, in which he stated that a basic sensorimotor and cognitive representation is a prerequisite for developing a language representation. However, Bruner's (1964) conceptualization was a one-way road compared to a neuroconstructivist perspective, which assumes that verb acquisition can change the constraints of neural language processing, which in turn affects how the MNS processes an observed action. This shows that the various levels and domains are interrelated because they influence each other's development and processing (Westermann et al., 2007). Importantly, such a perspective broadens Bruner's (1964) step-wise account of the development of representational systems because it not only proposes that cognitive representations build the basis for language representations but also that language representations affect and enrich cognitive representations. Therefore, a clear subdivision into cognition and language might not be the best way to describe representations as this suggests two rather independent and distinct domains. Rather, at least in the case of action perception, I would suggest that we represent communicative signals of different modalities in one overarching representation.

4.4. Limitations and future directions

In the previous sections, I have argued that Studies 1 and 2 provide evidence for the assumption that the MNS contributes to the processing of various communicative signals (i.e., actions and language). More specifically, this contribution consists in hypothesis testing, according to predictive coding (Kilner et al., 2007b). Furthermore, I have offered a proposal why associative learning is a possible foundation for the MNS as hypothesis testing system. Nevertheless, there are many questions that are still unanswered or that have come up in the process of conducting Studies 1 and 2. I will discuss some study-specific limitations, before I come to a more general concern with regard to how research investigates the processing of communicative signals and the role of the MNS in this process.

First, much research is still needed to comprehend the role of the MNS in processing communicative signals such as language and extracting meaning from these signals. There is an ongoing debate about the usefulness of the embodiment approach. The criticism is directed foremost to the retrieval of meaning and the necessity of the MNS for general language comprehension, that is, the grounding of language in action (Caramazza et al., 2014; Zwaan, 2014). It has been stated that the MNS might as well be active during the processing of communicative signals, as argued by embodied cognition, but this does not necessarily imply that the MNS is the cause for the retrieval of meaning and that language is grounded in action (Caramazza et al., 2014). According to this perspective, language representations and cognitive action representations are correlated due to the meaning of the verbs. Because of this proposed correlation, the MNS gets involved when action verbs are processed, but this involvement is argued to be only a byproduct of language processing (Caramazza et al., 2014) However, as stated previously, the question is whether it is useful to divide action and language into two domains and whether a language domain is grounded in the action domain. An alternative view is that action and language are not two domains but two facets of communication (Rączaszek-Leonardi et al., 2018). Therefore, it is not a question of if and how language is grounded in action but how communication is grounded in communication, and how this helps us to have successful social interactions (Rączaszek-Leonardi et al., 2018). Communicative signals are claimed to structure the environmental input, thus they facilitate processing, which is in line with neuroconstructivism stating that each level of the hierarchy constrains other levels in the hierarchy (Rączaszek-Leonardi et al., 2018; Westermann et al., 2007). However, it is still a valid question what facets of a communicative signal, such as an action verb, are used to constrain processing and to make social interactions successful. The findings from Study 1 provide support in favor of the grounding of linguistic communication in non-linguistic communication, but this support is limited to the difference of processing in the MNS for dynamic action verbs that are contrasted with pseudoverbs. This means that meaning including a dynamic component is confronted with no meaning at all. In order to get a clearer picture of the role of the MNS in the processing of meaning in general, one would need to test other conditions, such as static verbs and abstract verbs that are acquired at an early stage. A first step in this direction has been taken by Study 2, which used neutral linguistic expressions. However, the role of action-dynamics in action verb processing is only poorly understood in toddlers who have just acquired their first verb repertoire. I have also mentioned this issue earlier in this thesis, when discussing the nature of an action representation. It is still an open question what the action verb contributes to an action representation and which component of the action representation is most important to process an action verb; the holistic meaning of the action or the way how the action is performed (i.e., effector limb somatotopy). In future studies, this aspect could be clarified by experimentally manipulating these two types of meaning as well as by means of a measurement method that is more suitable to represent differences in location of brain activation than it is the case for EEG. Functional near-infrared spectroscopy might be a suitable measurement technique because it provides a better spatial resolution than EEG but is still much less invasive than classical methods to locate brain activity such as fMRI (Wilcox & Biondi, 2015). This is an especially important aspect for studies in developmental populations.

Second, the current dissertation project proposes that the function of the MNS in processing communicative signals lies in predictive coding rather than the retrieval of meaning. However, the evidence for predictive coding provided by Studies 1 and 2 is rather general. For instance, it remains to be assessed how the updating mechanism of previously made predictions works. This holds true in general but especially for research in early development. A shortcoming of Study 2 is that it does, in my view, not distinguish between the prediction and the updating of the prediction. This issue might be solved with further analyses in a different frequency band because it has been suggested, at least in adult literature, that the beta band best reflects this updating procedure by representing the prediction error (Braukmann et al., 2017; Palmer et al., 2016). Furthermore, the study testing incongruence effects of referential predictions on action predictions (Antognini & Daum, 2018) could potentially provide some insights about beta desynchronization as indicator for the size of the prediction error because the divergence between conditions is even stronger than in Study 2.

Third, I argued that Studies 1 and 2 provide evidence for the assumption that associative learning lies at the basis of predictive coding and of the MNS as processing system for communicative signals. This is in line with literature on this topic (Press et al., 2011). However, I am aware of the fact that this argument needs to be corroborated by more and more direct evidence because Studies 1 and 2 can only make claims about MNS processing of action verbs after the association with an action has taken place. More direct evidence could come from an associative learning study, similar to Fargier et al.'s (2012) and Gampe, Brauer, and Daum's (2016) paradigm, in which toddlers acquire new verbs in an experimental setting. This allows for measurements pre and post learning in the same individual. Furthermore, this paradigm offers many possibilities with respect to the manipulation of experience (i.e., experience with action verb, experience with action itself).

The three limitations mentioned are very specific to the studies conducted as part of this dissertation project. However, I would like to share a much bigger concern I have about research regarding processing of communicative signals. Currently, research tries to model a dynamic multilevel process, namely understanding within a hierarchical prediction system, with quite static and restrictive experimental designs. These restrictive designs, under which we might also subsume Studies 1 and 2, provide important insights about single puzzle pieces of a constructivist process. I have already argued that the puzzle pieces which were found in this dissertation project point to the fact that neuroconstructivism is a potential mechanism to describe the development of understanding communicative signals. This means that it might be fruitful to dig a little deeper into the mechanism. However, to do so, research needs different procedures, which are richer, more dynamic, and more flexible. Because the human brain, understanding, communication, and other social functions are dynamic, we need methods that can deal with dynamics and multiple layers of abstraction. Furthermore, there is a need for research investigating specifically the development of communication understanding because Studies 1 and 2 only provide snapshots of single points in development. They are not designed to represent development as a process, taking place within an individual, who grows up in and interacts with a certain (social) environment.

I would like to propose two possible ways of studying development under the premise of neuroconstructivism. The first possibility is neurorobotics. Neurorobotics allows us to study development on a fine-grained level, with an almost infinitely high resolution, in a context of embodiment (Prescott, Ayers, Grasso, & Verschure, 2016). This context of embodiment, that is, the relationship between brain processing, a body, and an environment, is an advantage neurorobotics has over computer models, which work without the bodily context (Prescott et al., 2016). In neurorobotics, different models of learning can be tested, which helps us to investigate how representations are built and how they are used in later processing (Park, Lim, Choi, & Kim, 2012). As neurorobotics works with artificial neural systems, one can study how "neural patterns" are processed on every level of the hierarchy. However, neurorobotics has a disadvantage that is unresolved to date: it has difficulties to model the social component of human life, although research on human-robot interaction in learning is trying to close this gap (Lallee, Madden, Hoen, & Dominey, 2010). The lack of the social environment and interaction is an especially big concern because it has been argued that development always happens within a social context, and every communicative signal is learned and dealt with in this context (Rączaszek-Leonardi et al., 2018). Furthermore, the interaction with an environment, or more general, the interaction between all layers within a hierarchy is a particular feature of an autopoietic system as proposed by neuroconstructivism (Westermann et al., 2007). Therefore, we would need to rebuild the whole context, even aspects that seem not relevant at first glance, in order to model how communicative signals are processed and interpreted. To sum up, this suggests that neurorobotics might be a good start to test different models of learning and neural processing, but it has still disadvantages that make it not the optimal or sole way to study the processing of communicative signals in development.

The second possibility is to study the development of processing communicative signals through studies within few individuals, potentially accounting for many possibly influencing factors. To do so, one would need to record as much information as possible from each layer, proposed by neuroconstructivism, at many time points (i.e., microgenetic design). This includes contextual information, which could be acquired by a diary app (see also "kleineWeltentdecker-App", 2018), as well as information about neural activity during the processing of communicative signals. This information can subsequently be used to build models about development, the dynamic interaction between the layers, and the role of the MNS within processing communication. This is a very challenging and laborious approach. Therefore, we might start using the neurophysiological data we have available from individuals who are learning and developing in social contexts (different from neurorobotics models) and use this data to build more flexible and dynamic models. A possible way of doing so is multivariate pattern analysis (MVPA), which can represent how representations are formed and tested (Haxby, 2012; King & Dehaene, 2014). MVPA is a method originally used in fMRI research, but it can be readily applied to other multidimensional data to obtain information about the fine-grained patterns in the data (King & Dehaene, 2014). Furthermore, MVPA is especially suitable for datasets with high interindividual variability (King & Dehaene, 2014), which is especially important for research on development. Therefore, I propose that MVPA might give new insights on the processing of representations as well as in the development of this processing. This technique would allow us to test theoretical models like predictive coding making use of the richness of EEG data we have available, that is, using all recorded time points, on all electrodes, and on a broad range of frequencies (King & Dehaene, 2014). For instance, a recent study in adults using MVPA has demonstrated that predictive coding is the mechanism underlying the processing of movement trajectories (Hogendoorn & Burkitt, 2018). Furthermore, I propose to run multiple MVPAs at multiple time points in order to use this information to build models about change of patterns, and thus about the development of action-representation processing. In my view, this is a very important and necessary step in the investigation of development and of the process of understanding. New methods allow us to represent dynamic processes or change and help to resist the temptation to study the end results of a process, instead of the process itself.

5. Conclusion

This dissertation project investigated the function of the MNS for the processing of different communicative signals in early language development. It has been shown that the MNS processes different communicative signals, such as actions and language from early on. This means the toddler in the introductory example used his MNS to process the parent's utterances as "I want to cut some shapes" as well as the parent's actions like transporting the cutter to the modeling clay to cut some stars. The MNS applies predictive and updating functions in order to understand communication and to constantly develop this understanding (Kilner, 2011; Lupyan & Clark, 2015). This explains how the toddler was able to hand over the cutter although it had not been explicitly requested (e.g., “Give me the cutter, please”) but implicitly implied because one needs a cutter to cut some shapes. Furthermore, we could witness the predictive functions in the gaze behavior of the toddler after the parent got the cutter.

The dissertation project has provided evidence that communicative signals are processed using cognitive representations of actions. Such action representations are rich and multimodal cognitive contents that are an inherent part of understanding communication in social interactions. Through this multimodality, communicative signals, such as actions and language, are interrelated facets rather than independent domains (Barsalou, 2008; Bruner, 1964). Therefore, the dissertation project adds to the long-standing discussion about the interrelation or independence of cognition and language in general. That is, language development is closely related to social-cognitive development (Tomasello, 2003). Overall, this dissertation project contributes to a deeper insight in the working of social interactions and the role of the brain as a hypothesis testing system in this context.

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Part II

A) Study 1: Toddlers show sensorimotor activity during auditory verb processing

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Abstract

Language that describes actions, for instance verbs, can help to predict future actions of conspecifics in social interactions. Language and action are therefore interrelated. This interrelation has been described on a behavioral level for adults and toddlers. Furthermore, in adults, the sensorimotor system is involved in this interrelation. However, little is known about the early interrelation on the neural level at the onset of verb acquisition. In the present study, we examined the role of the sensorimotor system during the processing of acoustically presented verbs that describe dynamic actions and visually presented actions in toddlers, who are in the earliest stage of expressive language development. The activity of the sensorimotor system, in particular the suppression of the mu rhythm, was measured by means of electroencephalography (EEG). Results showed a significant suppression of the mu rhythm during both the processing of action verbs and observed actions, but not during the processing of pseudoverbs. This suggests that the sensorimotor system is already involved in the processing of action and language early in life.

Key words: Language; Action Perception; Embodiment; Mu Rhythm; Mirror Neuron System; Development

1. Introduction

Language, and more specifically verbs, are an inherent part of social interactions (Tomasello, 2001). In social interactions, verbs can serve as cues to predict future behavior, especially future actions of conspecifics (Springer, Huttenlocher, & Prinz, 2012). It has been demonstrated that action processing and verb processing are interrelated in adults (Fischer & Zwaan, 2008; Pulvermüller, 2005; Springer et al., 2012) and toddlers (Gampe & Daum, 2014; Gampe, Brauer, & Daum, 2016). In adults, extensive literature shows that the sensorimotor system is involved in this interrelation (Buccino et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; Mollo, Pulvermüller, & Hauk, 2016; Moreno, de Vega, & León, 2013; Rüschemeyer, Brass, & Friederici, 2007; van Elk, van Schie, Zwaan, & Bekkering, 2010), resulting in similar brain activations during the production and the visual observation of actions, as well as during listening to action-related verbs. However, it is less well studied how this interrelation develops, and which neural systems are involved. The aim of the present study was to investigate whether sensorimotor involvement in both action and verb processing is already established in toddlers, who are at the beginning of verb acquisition. This study is an important first step towards increasing our understanding of the early interrelation between action and language, since it investigates whether the sensorimotor system underlies the processing of different modalities (linguistic and visual) of action representations, as has been reported in adults already (Pulvermüller, 2005). This means that we study the interrelation of action and language in light of a common neural processing system for different action representations. In the following, we briefly introduce the importance of studying the interplay between language and action from a general, and in particular, from an ontogenetic perspective, focusing on the development of this interplay with a focus on verb acquisition in early childhood. Furthermore, we highlight the commonalities of action and verb processing on a neural level.

Verbs belong to a lexical category that reflects activities, processes, and relations, and as such they are distinct from nouns, which describe entities (Baker, 2003; Golinkoff & Hirsh-Pasek, 2006; Tomasello, 1992). These processes and relations can be concrete and dynamic (e.g., running, grasping), static (e.g., standing, waiting), or abstract (e.g., existing, thinking). In the following we focus on dynamic action verbs, since toddlers' first-acquired verbs are to a great extent verbs that describe observable actions of people, such as drawing and stacking (Golinkoff & Hirsh-Pasek, 2006; Sootsman Buresh, Woodward, & Brune, 2006). Abstract verbs are not acquired until later on (Kauschke, 2012). In addition, for reasons of brevity, when writing *verbs* we refer to these dynamic action verbs. Consequently, we consider early-acquired verbs as a linguistic form of action representations, and as such junctions in which actions and words come together (Golinkoff & Hirsh-Pasek, 2006).

Since verbs and actions are semantically related, and verb acquisition consists of mapping words onto actions (Gentner & Boroditsky, 2001), it seems feasible that verb acquisition does not reflect a process whose development is isolated in the language domain, but is rather closely related to development in the action domain. For instance, one needs to understand an action and its facets to learn the label that maps onto the action (Sootsman Buresh et al., 2006). Therefore, verb acquisition builds on a range of action perception skills, such as the processing of motion, action goals, or intentions (Pulverman, Hirsh-Pasek, Golinkoff, Pruden, & Salkind, 2006). These action perception skills are acquired early on in development, at a prelinguistic stage. For example, the detection of biological motion and the preference for it is an intrinsic ability already present in newborns (Simion, Regolin, & Bulf, 2008). From about 6 months of age, infants perceive actions as being directed towards goals (Biro & Leslie, 2007; Daum, Prinz, & Aschersleben, 2008, 2009; Luo & Johnson, 2009; Woodward, 1998). Furthermore, perceiving actions and their goals is already associated with activity in the sensorimotor system of the brain from a very young age. It has been reported that infants from the age of 8 months show activity in the sensorimotor system during the observation of someone else's actions (e.g., Marshall, Young, & Meltzoff, 2011; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Southgate, Johnson, Osborne, & Csibra, 2009; Warreyn et al., 2013). The sensorimotor system is thus involved in action perception, which is a basis for verb acquisition (Pulverman et al., 2006).

Later on in development, these early action-perception skills serve to map words onto perceived actions, and in turn to acquire verbs (Sootsman Buresh et al., 2006). Verb comprehension starts at the beginning of the second year of life (Golinkoff & Hirsh-Pasek, 2008) and precedes verb production, which increases at around 18-24 months of age (Kauschke, 2012; Rothweiler & Kauschke, 2007). Furthermore, toddlers reach a total vocabulary of approximately 100 words at this stage (Bates et al., 1994). So an increase in expressive verb vocabulary is not only associated with an increase in age but also with an increase in general language repertoire, i.e. overall vocabulary (Kauschke, 2012).

In adults, who are highly proficient in using verbs, not only temporal and inferior frontal language-processing areas are involved in verb processing, but also the sensorimotor system (Buccino et al., 2005; Hauk et al., 2004; Moreno et al., 2013; Repetto, Colombo, Cipresso, & Riva, 2013; Rüschemeyer et al., 2007; van Elk et al., 2010). However, the sensorimotor system is only involved in verb processing if verbs map closely onto actions, which is the case for action verbs, but not for abstract verbs or pseudoverbs (Buccino et al., 2005; Fargier et al., 2012; Hauk et al., 2004; Moreno et al., 2013; Repetto et al., 2013; Rüschemeyer et al., 2007; van Elk et al., 2010). Abstract verbs describe mental states and processes (e.g., thinking, doubting, believing; Moreno et al., 2013), whereas pseudoverbs are novel and have no semantic content (Fargier et al., 2012). Both stand in contrast to action verbs, which describe movements of body parts. Furthermore, the sensorimotor system processes action verbs similarly to observed actions (Moreno et al., 2013). This indicates that the sensorimotor system processes different action representations from the action and the language domain. In addition, similar findings have also been reported for the processing of action-related sounds (Kohler et al., 2002; McGarry, Russo, Schalles, & Pineda, 2012; Pineda et al., 2013). Short-term training of pseudoverb-action associations can also induce the sensorimotor mapping of a novel verb onto an unfamiliar action (Fargier et al., 2012). This indicates that, in adults, sensorimotor processing of verbs can result from associative learning (Cooper, Cook, Dickinson, & Heyes, 2013; Heyes, 2010). Verbs that have been mapped onto actions, either by short-term training or life-long experience with language, are thus associated with sensorimotor activity in adults. In this study, we investigated whether this also holds true for toddlers who are at the beginning of this mapping process. Adults have an immense repertoire of verbs and actions at their disposal which is based on their lifetime experience with both language and actions. In contrast, early in life, children are in the process of acquiring proficiency in both language and action. The question is, therefore, under which circumstances (e.g., motor skills, language status) the sensorimotor system starts to become involved in the processing of different action representations, such as observed actions, action sounds, or action verbs in early development.

Similar to the associative learning reported in the context of pseudoverbs in adults (Fargier et al., 2012), associative learning can result in sensorimotor processing of action-related sounds in 7- to 9-month-olds, who displayed activity in sensorimotor brain regions for sounds that had been associated with shaking actions in a training phase (Gerson, Bekkering, & Hunnius, 2015; Paulus, Hunnius, & Bekkering, 2013; Paulus, Hunnius, van Elk, & Bekkering, 2012). It was postulated that sensorimotor activity in response to sounds is the result of an association between the shaking action and the effect of the shaking (Gerson et al., 2015; Paulus et al., 2012). If this association becomes strong enough, the perception of the action effect triggers sensorimotor activity (Cooper et al., 2013; Heyes, 2010). These findings provide evidence for the assumption that associative learning already plays a role in the sensorimotor processing of different action representations early on in development (Gerson et al., 2015; Paulus et al., 2013, 2012). Additionally, first-hand experience with actions influences the strength of association between different action representations (Locatelli, Gatti, & Tettamanti, 2012). For instance, action sounds were associated with stronger sensorimotor activity when they were linked to actually produced actions than to merely observed actions (Gerson et al., 2015). Also, sensorimotor activity in response to observed actions is stronger when the infant is able to perform the action (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008; Yoo, Cannon, Thorpe, & Fox, 2016). This effect could be explained with the potential strength of the representations of an action. Representational strength is a concept within the account of graded representations, where strength depends on experience with a given entity that is represented (Munakata, McClelland, Johnson, & Siegler, 1997). Furthermore, strong representations provide clean neural signals that allow connections to other representations in the cognitive system: For instance, strong motor representations of an action allow connections with auditory representations of an action (i.e., sound that is elicited by performing the action). On a neural level, the graded representations account states that representational strength could be operationalized by neuronal firing rates, firing coherence, and connectivity (Munakata, 2001). Previous research showed that experience influences representational strength, for example of objects; that is, object representations are stronger if infants are more experienced in perception of and interaction with the objects (Shinskey & Munakata, 2005). Furthermore, representational strength increases with age, which can again be explained by extended experience with increasing age (Munakata, 2001). At the age of 22 months, toddlers retrieve and update representations more easily than at 19 months (Ganea, Shutts, Spelke, & DeLoache, 2007). For the present study, we assume a similar association between experience, representational strength, and sensorimotor involvement for linguistic action representation as has been reported for visual action representation. Consequently, we expect the sensorimotor response to verbs to be stronger for verbs that a toddler is able to vocalize in contrast to verbs that are either only part of the toddler's receptive vocabulary or that are unknown, such as pseudoverbs. Similar to the retrieval of object representations from memory (Ganea & Saylor, 2013), the retrieval of the meaning of a verb from memory will then be better for verbs that are more strongly represented. This means that sensorimotor involvement in verb processing could be associated with proficiency or experience in using verbs.

As mentioned above, adults, who are proficient verb users, show sensorimotor involvement in verb processing (Buccino et al., 2005; Hauk et al., 2004; Moreno et al., 2013; Repetto et al., 2013; Rüschemeyer et al., 2007; van Elk et al., 2010). In addition, a functional magnetic resonance imaging study already showed sensorimotor processing for auditorily presented action verbs in preschoolers (4-5 years old), who have a smaller expressive verb repertoire than adults (James & Maouene, 2009).[1] More specifically, the preschoolers' sensorimotor system showed somatotopically distributed activity corresponding to the effector limbs used to perform the action described by the verb (James & Maouene, 2009). Similar somatotopic activation patterns are reported in studies with adult participants (Pulvermüller, 2005). However, 4- to 5-year-olds still have already well-developed action and verb repertoires, which are smaller, but far closer to the adult repertoires than to those of toddlers, especially with respect to the simple actions and action verbs used in the studies. It therefore remains unclear whether the sensorimotor system also plays a role in the processing of verbs in early stages of verb acquisition.

We investigated this question by examining sensorimotor activity during action-verb processing in 18- and 24-month-olds. We assumed that toddlers in both age groups have already acquired some basic receptive action-verb repertoire (Golinkoff & Hirsh-Pasek, 2008), but still differ in their expressive action-verb repertoire (Bates et al., 1994). We acoustically presented sentences with early-acquired action verbs and pseudoverbs, and showed video clips of means-end actions. Pseudoverbs are an ideal control condition for two

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[1] The modality of stimulus presentation was different from studies in adults, which mostly use visual presentation of verbs (e.g., Hauk, Johnsrude, & Pulvermüller, 2004; Moreno, de Vega, & León, 2013).

reasons. First, in adults, pseudoverbs were not associated with sensorimotor activity (Fargier et al., 2012). Second, unlike abstract verbs, pseudoverbs do not carry semantic information but have still a valid phonotactic structure in contrast to non-words (Friedrich & Friederici, 2005). During stimulus presentation, the toddlers' sensorimotor activity was assessed by means of electroencephalography (EEG). Early-acquired action verbs were defined according to normative data as verbs that, on average, are in the expressive verb repertoire of 15 % of 18-month-olds and 60 % of 24-month-olds (Szagun, Stumper, & Schramm, 2009). Sensorimotor activity was measured by suppression of the mu rhythm, which is within the alpha range and is typically present over central electrode sites (Hobson & Bishop, 2016; Marshall & Meltzoff, 2011). The mu rhythm is strongly present in the EEG signal when the sensorimotor system is at rest, but gets suppressed when the system is activated (e.g., during action production or perception; Cuevas, Cannon, Yoo, & Fox, 2014). In infants, the frequency band of interest is 6-9 Hz (Marshall, Bar-Haim, & Fox, 2002; Stroganova, Orekhova, & Posikera, 1999), which is lower than in adults (8-13 Hz; Marshall & Meltzoff, 2011). Studies report a gradual increase in the peak frequency with increasing age. It has been reported that the peak frequency is about 8 Hz at 24 months of age (Berchicci et al., 2011; Marshall et al., 2002). Despite this difference in the frequency range, the function and topography of the mu rhythm are similar in infants, toddlers, and adults (Marshall & Meltzoff, 2011).

The following three main questions guided the present research: First, do toddlers show a suppression of the mu rhythm when listening to action verbs similar to the reported suppression when observing actions (Warreyn et al., 2013)? We expected this to be the case, since toddlers already have a receptive vocabulary of action verbs (Golinkoff & Hirsh-Pasek, 2008) as verified by a parent questionnaire, and therefore associations between actions and verbs are established. Second, is the suppression of the mu rhythm different in response to action verbs than to pseudoverbs? The adult sensorimotor system responds to pseudoverbs only after associations with actions have been formed by training (Fargier et al., 2012). However, it remains an empirical question whether pseudoverbs are associated with sensorimotor activity or not in toddlers. One possibility is that pseudoverbs are recognized as verbs describing an (as yet unlabeled) action due to their morphology, and are therefore processed similarly to action verbs that are already in the child's vocabulary (Hernandez Jarvis, Merriman, Barnett, Hanba, & van Haitsma, 2004; Mani, Durrant, & Floccia, 2012). Another possibility is that pseudoverbs are not associated with sensorimotor activity in toddlers, since the pseudoverbs do not map onto actions, which would parallel findings from a study in adults (Fargier et al., 2012). Third, is the suppression of the mu rhythm in response to verbs different for 18- and 24-month-olds? Within this age range, toddlers differ with respect to expressive verb repertoire (Bates et al., 1994), which might affect sensorimotor activity in response to verbs depending on age. There is evidence that greater expressive vocabulary was associated with implicit production of nouns that fit a preceding verb (Mani, Daum, & Huettig, 2016; Mani & Huettig, 2012). It is a feasible assumption that this task includes mental simulation of the action described by the verb, which facilitates the prediction of the appropriate noun or object. If a greater expressive verb vocabulary – and in turn more experience with verbs and hence stronger verb representations (Munakata, 2001; Shinskey & Munakata, 2005) – is associated with better mental simulation of the action, we could assume that the suppression of the mu rhythm is stronger for toddlers with a larger expressive verb vocabulary. This is because the suppression of the mu rhythm is related to mental simulation of actions (Jeon, Nam, Kim, & Whang, 2011; Nam, Jeon, Kim, Lee, & Park, 2011; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; Pineda, Allison, & Vankov, 2000). However, the strength of the sensorimotor verb-action association could depend rather on motor experience with the action than verb repertoire. We know that motor experience is essential to form associations between actions and action effects (Gerson et al., 2015). Accordingly, it is plausible to hypothesize that motor experience is beneficial for the formation of an association between the action and the corresponding verb. However, we assume that both age groups have similar motor experience with the particular actions that were presented to the children in the present study. This implies that the two age groups are not expected to differ with respect to the suppression of the mu rhythm in response to action verbs.

2. Materials and Methods

2.1 Participants

We included 20 toddlers (7 female) aged 18 months (M = 566.6 days, range = 551-579 days) and 27 toddlers (15 female) aged 24 months (M = 747.2 days, range = 724-777 days) in the final sample. All toddlers provided a minimum of six trials per condition and completed at least the first block of the procedure (verb block). This sample was used for the analysis involving the first block. In total, an additional 28 toddlers aged 18 months and 20 toddlers aged 24 months were tested but excluded due to technical problems (n = 1), refusal to keep the net on their head (n = 5), or because they did not provide enough artifact-free trials (n = 42). The average attrition rate of 50.5% was within the expected range for this age group (DeBoer, Scott, & Nelson, 2013) and comparable to other studies in the field (Bache et al., 2015; Reid, Striano, & Iacoboni, 2011; Stapel, Hunnius, van Elk, & Bekkering, 2010; Warreyn et al., 2013). To compare the neural response to verbs and observed actions, we selected a subsample of toddlers (n = 33) who completed both blocks of the procedure (verb block and observation block), satisfying the criterion of a minimum of six trials per condition in both blocks. This subsample consisted of 14 18-month-olds (4 female) and 19 24-month-olds (10 female).

All toddlers were recruited from local birth records. They were born full term (week of gestation ≥ 37), had normal birth weight (≥ 2500 g), grew up in Swiss-German monolingual households and had right-handed parents. The study was approved by the local ethics committee. Caregivers gave written informed consent. The toddlers received a small age-appropriate toy (value equivalent to 5 USD) and a printed certificate for their participation in the study.

2.2 Stimuli

We used three types of materials: auditory stimuli, visual stimuli, and play material. The auditory stimuli consisted of six sentences spoken by a native Swiss-German female speaker. The full duration of each sentence was 1100 ms. The sentence structure was as follows: "Ich" [I] from 0-400 ms and a verb (action verb or pseudoverb) from 500-1100 ms after sentence onset. We used three different familiar action verbs: "maale" [to draw], "schniide" [to cut], "baue" [to build]. These had been chosen because they were classified as early-acquired verbs according to the Swiss-German adaptation the language questionnaire FRAKIS (Szagun et al., 2009). The corresponding pseudoverbs were constructed such that they had the same initial sound and end sound as the familiar action verb: "mieke", "schraade", "bope".

The visual stimuli consisted of video clips depicting means-end actions that corresponded to the familiar action verbs used in the auditory stimuli. The video clip showed an actress's arms, hands, and torso from a third-person perspective. The actress sat at a table with two objects lying in front of her. The object near her right hand (i.e., on the left side of the screen) was always the means object (e.g., green pencil, plastic toy knife, blue wooden building block), whereas the object near her left hand (i.e., on the right side of the screen) was the goal object (e.g., yellow piece of paper, orange toy carrot with three pieces held together by Velcro, two stacked yellow and red wooden building blocks). The structure of the actions was as follows (see Fig. 1): The actress sits at the table with her hands in a resting position (0-600 ms). Then, she lifts her right hand and grasps the means object (2100 ms), which is transported towards the goal object. On arrival at the goal object (3500 ms), she performs the appropriate action. After finishing the action (5400 ms), she puts the means object down and returns her hands to the resting position. All these steps taken together resulted in a 6000 ms video clip. As play material, we used the same objects as shown in the video clips of the means-end actions.

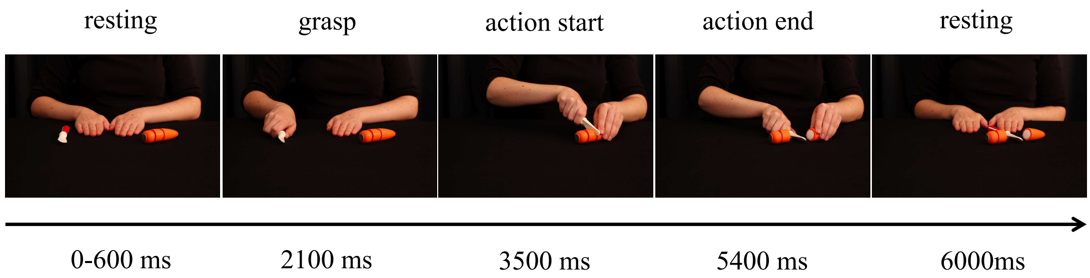

Fig. 1. Structure of the video clips. Here, the action *to cut* is depicted with respect to the action boundaries resting, grasping and action execution. The structure of the other actions was analogous.

2.3 Procedure

On arrival at the lab and as part of the standard procedure, the caregivers were asked to provide information about years of education and handedness of both parents. Furthermore, to assess action-verb production, the caregivers were asked to indicate whether the toddler understood and spontaneously produced (i.e., vocalized) the action verbs that were presented in the EEG paradigm. Verb comprehension was not assessed directly, since parent reports have poor validity, especially for the second year of life (Eriksson, Westerlund, & Berglund, 2002; Feldman et al., 2005; Tomasello & Mervis, 1994). Language status was not assessed otherwise. Moreover, caregivers were asked to indicate whether the toddler performed the actions that we used in the EEG paradigm in their daily lives or during playtime.

The EEG paradigm took place in a dimly lit, electrically shielded and sound-attenuated room. The toddler sat on the caregiver's lap, at an approximate distance of 60 cm from a 17-inch computer screen with adjacent loudspeakers. We used the software Presentation 18.1 (Neurobehavioral Systems, USA) to present the auditory and visual stimuli. The EEG paradigm consisted of two separate blocks, which were always kept in the same order. The verb block came first, followed by the observation block. The order was kept constant to exclude any possible carry-over effects from action observation onto verb processing.

In the verb block, the trials were presented in random order, with a maximum of three trials of the same condition (action verb, pseudoverb) in a row. Throughout the sentence presentation, a red dot with a diameter of about 3 cm was presented in the middle of the screen. In addition, this dot served as a fixation point in the between-stimulus interval (BSI), which had a duration of 2000 ms. During the sentence presentation as well as the BSI, the dot changed its color gradually from red to yellow and back to red. The gradual color change was chosen to keep the toddlers' quiet attention using a changing stimulus (Cuevas et al., 2014) that is not associated with an action, since there was no translational movement or contingency with any other stimulus. We suppose that the gradual color change is therefore not interpreted as action. After every third trial, or if the toddler became inattentive, an attention grabber was presented. Attention grabbers consisted of a video depicting a spiraling screensaver with a jingling sound. The verb block consisted of a maximum of 60 trials (30 trials per condition), but was terminated by the experimenter if the toddler was not attending to the stimuli anymore (i.e., inattention for more than 6 trials in a row).

The observation block was divided into three sub-blocks with respect to the three actions that were used as action verbs in the verb block. The order in which the sub-blocks were presented was randomized. For each action, the video clip was presented six times in a row. The BSI in the observation block was identical to the BSI in the verb block in terms of the stimulus shown and the timing. After these six identical video clips, the experimenter handed the toddler the play material that the actress had used in the video clip. By saying "It's your turn!", the experimenter prompted the toddler to imitate the action shown in the video clip. The imitation trial ended after the toddler had completed the action, or if the toddler did not initiate the action after 15 seconds.

The imitation trials were used to maintain the toddlers' attention, but EEG was not further analyzed.[2] Because of these imitation trials the aforementioned subdivision into sub-blocks was necessary in order to avoid carry-over effects from the imitation of an action onto the observation of the action.

2.4 EEG recording and analysis

The EEG was recorded with a NetAmps 300 amplifier (Electrical Geodesics Inc., Eugene, OR, USA) at 500 Hz sampling rate and a 128-channel sensor net with infant layout (Electrical Geodesics Inc., Eugene, OR, USA). During recording, an online 0.1 Hz high-pass filter was applied and data were referenced to the vertex. Impedances were kept below 50 kΩ.

After EEG acquisition, the data were preprocessed in the EEGLAB toolbox (Delorme & Makeig, 2004). We applied a 0.3-30 Hz band-pass filter and removed the outermost channels (due to insufficient contact with the scalp; Filippi et al., 2016; Nyström et al., 2011). Trials in which the toddler moved or did not attend to the stimuli were removed. In the verb block, on average 51% of the epochs from the action-verb condition and 48 % of the epochs from the pseudoverb condition were removed. In the observation block, on average 43 % of the epochs were removed. We performed an independent component analysis (ICA) to identify and remove artifacts due to eye movements, sweating, and heartbeat (Delorme &

[2] Initially, we intended to analyze the EEG data from the imitation condition to have a measure for action execution (Cuevas, Cannon, Yoo, & Fox, 2014). However, we did not obtain enough trials for the analysis because of very strong movement artifacts, mostly due to head movements and because toddlers refused to interact with the play material.

Makeig, 2004). Finally, we interpolated missing channels using spherical interpolation and re-referenced the data to common average reference.

Data from the verb block were segmented according to condition (action verb, pseudoverb). We extracted 2500 ms epochs, consisting of 1000 ms before sentence onset and 1500 ms after sentence onset. On average, we obtained 12.5 trials for the action-verb condition (range = 6-24) and 12.7 trials for the pseudoverb condition (range = 6-26). Data from the observation block were segmented into 8000 ms epochs with a 1500 ms period before and a 6500 ms period after video onset. We obtained an average of 9.6 trials for the action-observation condition (range = 6-16).

Data were analyzed in Matlab (R2014b) by performing a time-frequency analysis over a frequency range between 4 and 20 Hz using Morlet wavelets with constant 5 cycles and windowed with a cosine square window. The analysis provided raw power values [μV^2] that were then averaged over trials. We calculated the mean power over a frequency band between 6-10 Hz. This frequency band was chosen because at 24 months of age the peak frequency has been reported to be at about 8 Hz (Berchicci et al., 2011; Marshall et al., 2002). We chose a frequency band with ± 2 Hz around this peak frequency. Extracting individual frequency bands from the imitation trials, as suggested in the literature (Cuevas et al., 2014), was not possible because most imitation trials were highly contaminated with movement artifacts and many toddlers refused to interact with the play material. Furthermore, two time windows were selected, for which the average power was calculated over the time domain. For the epochs of the verb block, the first time window (baseline) represented the 0-400 ms period, where the "Ich" [I] had been presented. This baseline was chosen because it includes the same visual stimulation (color-changing dot) and auditory information that is not, however, a verb. This is to account for possible effects of hearing any type of vocalization on sensorimotor activity. The second time window represented the full verb period between 500-1100 ms. For the epochs from the observation block, we selected the first time window between -1000-0 ms (baseline), which represents the second half of the BSI. We chose only the second half of the BSI to exclude any carry-over effects from the trial before. A second time window considered the whole length of the video clip (0-6000 ms)[3].

Since we expected differences in activity over central sites, we selected two clusters of channels, which correspond to C3 and C4 in the 10-20 system (left central: E29, E30, E35, E36, E37, E41, E42; right central: E87, E93, E103, E104, E105, E110, E111). Furthermore, we selected an occipital cluster (E66, E69, E70, E74, E75, E76, E79, E82, E83, E84, E89) to show the specificity of our hypothesized effect to the central sites. The averaged raw power values [μV^2] were used to calculate event-related desynchronization (ERD) values according to Pfurtscheller (2001). We used the first time window in each of the conditions as the baseline period and the second time window as the activation period. Statistical analyses were performed with the R statistical package (R Core Team, 2016).

3. Results

3.1 Questionnaire data

We analyzed the language questionnaire data for all $n = 47$ toddlers in the final sample. A two-sample t-test for differences between the age groups in the expressive vocabulary regarding the words we used in the EEG paradigm indicated that the 24-month-olds produced (i.e., vocalized) the verbs significantly more often than the 18-month-olds, $t(45) = -8.91$, $p < .001$. Furthermore, we ran a two-sample t-test to analyze differences in action production of the actions that were used in the video clips during the EEG paradigm. Results indicated that there was no difference in action production between the two age groups, $t(45) = -0.957$, $p = .344$.

[3] Additionally, we selected a time window from 3500-5400 ms, which represents the period of time where the actress acts on the goal object. There was no difference between this time window and the full time window (grasping and action on goal object) with respect to sensorimotor activity, $F(1,31) = 1.78$, $p = .191$. Therefore, we did not further analyze this shorter time window, but instead the full video clip we presented.

3.2 EEG data

Firstly, we conducted an analysis for the verb block including all subjects with a minimum of 6 artifact-free trials per condition (action verb, pseudoverb). Secondly, we compared ERD between action verbs and action observation for those toddlers who provided a minimum of six trials per condition in both blocks (verb block, observation block). We chose this subsample because all toddlers have completed the verb block before the observation block. Thus, exposure to the corresponding action verbs was the same for this group of toddlers, which would not have been the case if we had chosen all toddlers who completed the observation block irrespective of the verb block.

3.2.1 Verb block

To answer our second question of whether action verbs and pseudoverbs differ in their involvement of the sensorimotor system, we ran a mixed-effects analysis of variance (ANOVA) on mean ERD values. The within-subject factors were condition (action verb, pseudoverb) and cluster (left central, right central, occipital). The between-subjects factor was age group (18 months, 24 months). This analysis revealed a significant main effect of cluster, $F(2, 90) = 4.66$, $p = .012$, $\eta_p^2 = 0.022$. No main effects for condition, $F(1, 45) = 1.40$, $p = .243$, or age group, $F(1, 45) = 0.210$, $p = .811$, were found. Further, results revealed an interaction effect between cluster and condition, $F(2, 90) = 3.26$, $p = .043$, $\eta_p^2 = 0.010$. No other interaction effects reached significance (all $p > .548$). To further analyze the interaction effect between cluster and condition, we conducted paired t-tests which indicated that ERD for action verbs ($M = -5.07$, $SD = 15.5$) was significantly different from ERD for pseudoverbs ($M = 4.97$, $SD = 29.2$) in the left central cluster $t(46) = -2.10$, $p = .042$ (see Fig.2), but not in the other clusters (all $p > .668$). Furthermore, one-sample t-tests indicated that ERD for action verbs was different from zero in the left central ($M = -5.07$, $SD = 15.5$), $t(46) = -2.24$, $p = .030$ and in the occipital cluster ($M = -7.41$, $SD = 14.8$), $t(46) = -3.44$, $p = .001$, while ERD for pseudoverbs differed from zero only in the occipital cluster (M = -6.07, SD = 15.8), $t(46)$ = -2.63, p = .011.

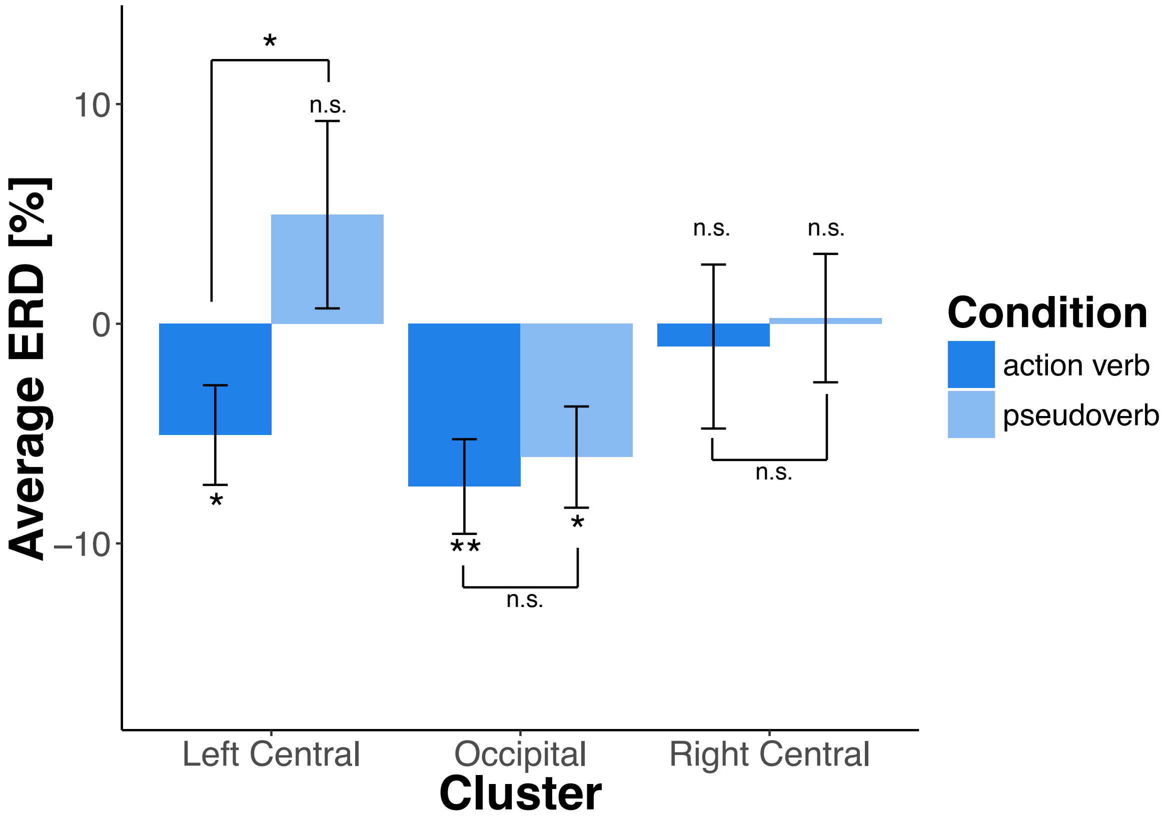

Fig. 2. Average ERD within the toddler mu range of 6-10 Hz for action verbs and pseudoverbs, split by electrode clusters. The ERD indicates % changes with respect to the baseline time window. Error bars indicate ±1 standard error. Significant differences are indicated by * = $p < .05$, ** = $p < .01$. Non-significant values are indicated by n.s.

3.2.2 Verb block compared to observation block

To answer our first question of whether action verbs and observed actions both involve the sensorimotor system, we compared the ERD for action verbs and for action observation in the sample of toddlers (n = 33), who completed both blocks satisfying the criterion of a minimum of 6 trials per condition. We ran a mixed-effects ANOVA including the within-subject factors condition (action verb, action observation) and cluster (left central, right central, occipital), and the between-subjects factor age group (18 months, 24 months).

With respect to the time window for action observation, we chose the full action period, since it did not differ from the period where the actress acted on the goal object. The results revealed a significant main effect of cluster, $F(2, 62) = 11.7$, $p < .001$, $\eta_p^2 = 0.063$. Furthermore, the results indicated an interaction effect between cluster and condition, $F(2, 62) = 21.9$, $p < .001$, $\eta_p^2 = 0.106$, and an interaction effect between age group and cluster, $F(2, 62) = 5.62$, $p = .006$, $\eta_p^2 = 0.031$. No other main effects (all $p > .073$) or interaction effects (all $p > .244$) reached significance.

To evaluate whether the conditions differed within the clusters, we ran paired t-tests on each cluster. In the right central cluster, ERD for action verbs ($M = -5.12$, $SD = 19.1$) was significantly weaker than ERD for action observation ($M = -26.43$, $SD = 14.4$), $t(32) = 5.26$, $p < .001$. In the left central and in the occipital cluster, ERD for action verbs and action observation did not differ significantly (all $p > .461$). One-sample t-tests indicated that ERD for action verbs was different from zero in the left central cluster ($M = -7.62$, $SD = 14.9$, $t(32) = -2.93$, $p = .006$) and in the occipital cluster ($M = -9.44$, $SD = 14.3$, $t(32) = -3.78$, $p < .001$). For action observation, one-sample t-tests indicated that ERD differed from zero in the right central ($M = -26.4$, $SD = 14.4$, $t(32) = -10.6$, $p < .001$) and in the occipital cluster ($M = -10.9$, $SD = 14.5$, $t(32) = -4.31$, $p < .001$).

To investigate whether ERD for age groups differed within clusters, and thus to answer our third question, we ran two-sample t-tests within clusters to compare the age groups. The results indicated that the difference between ERD for 18-month-olds ($M = -13.9$, $SD = 11.2$) and 24-month-olds ($M = -7.40$, $SD = 7.21$) was marginally significant, $t(31) = -2.02$, $p = .053$, in the occipital cluster. ERD scores did not differ between age groups in the other clusters (all $p > .095$).

4. Discussion

We investigated the involvement of toddlers' sensorimotor systems during the processing of acoustically presented verbs. Toddlers listened to sentences with phonologically similar action verbs and pseudoverbs, while the response of the mu rhythm was recorded using EEG. Additionally, to compare the brain responses between acoustically presented verbs and visually presented actions, we also recorded the mu rhythm response to observed actions.

In the following, we discuss the results of the current study with respect to our three main questions: First, do toddlers already show an activation of their sensorimotor system indicated by a suppression of the mu rhythm when listening to action verbs as they do when observing actions? Second, is the suppression of the mu rhythm different in response to action verbs than to pseudoverbs? Third, is the suppression of the mu rhythm in response to verbs different for 18- and 24-month-olds?

4.1 Suppression of the mu rhythm for action verbs in toddlers?

We first discuss the results concerning action verbs. Secondly, we discuss the neural responses for observed actions, and thirdly, we consider the similarities of neural responses to action verbs and observed actions.

4.1.1 Action verbs

We found a significant suppression of the mu rhythm over the left central electrode cluster in response to action verbs. However, this neural response was not specific to central sites, since we also found a suppression of the occipital alpha rhythm in response to action verbs. The central effect indicates that the sensorimotor system is active during the processing of action verbs. This effect was lateralized towards the left hemisphere. The lateralization of the mu suppression towards the left hemisphere can be interpreted in two different ways. Firstly, the activity of the sensorimotor system could be left-lateralized because the toddlers mentally simulate performing the action. We presume that our toddlers are right-handed, since we included only toddlers with right-handed parents in the sample and the probability of left-handedness when having two right-handed parents is very low (McManus & Bryden, 1992). Furthermore, the majority of the population is right-handed. Simulating the performance of an action like cutting with the right hand would fit a left lateralization of the suppression of the mu rhythm (Jeon et al., 2011; Nam et al., 2011; Pfurtscheller et al., 2006; Pineda et al., 2000). Secondly, one might interpret the left lateralization in terms of similarities with language processing. Action verbs are a linguistic form of action representation (Barsalou, 2008) and share some commonalities with general language processing, which is known to be left-lateralized in most right-handers (Knecht et al., 2000). This lateralized pattern for the processing of action verbs which we observed in our study has already been reported in adults (Hauk & Pulvermüller, 2011). It was shown that action verbs that indicate a uni-manual action were processed more strongly in the left central cortex for right- as well as left-handers. The authors argue that these results show that the processing of action verbs is more strongly associated with language lateralization, which is presumed to be mostly left hemispheric in both groups, than with handedness itself. In that study, many uni-manual action verbs were presented but amongst these were also the verbs cutting and drawing, which were also part of our paradigm (Hauk & Pulvermüller, 2011). Since we did not have an explicit measure of handedness or language lateralization, nor include left-handed toddlers, we cannot infer which of the two possible explanations is more likely. Future studies could investigate the role of handedness in action verb processing in toddlers.

An often-mentioned criticism regarding sensorimotor activity in response to action-verb processing concerns vocalization. This means that the sensorimotor activity during action-verb processing could not be associated with the motor-related meaning of the verb, but rather with the activity of the vocal tract and the mouth area of the motor cortex during the vocalization of the verb, independent of its meaning. Three reasons speak against this assumption. Firstly, we used a baseline also containing vocalization for the calculation of the ERD scores. We chose the baseline specifically to account for possible confounding effects of vocalization. Since ERD for action verbs was significantly different from baseline, a mere effect of vocalization can be excluded. Secondly, we have to specify whether it is necessary that the toddler be able to vocalize the action verb himself in order to show sensorimotor activity due to vocalization. A study on the relation between produced or observed actions and action sounds suggests that first-hand motor experience is a prerequisite for sensorimotor activity that is associated with the action sound (Gerson et al., 2015). This means for our study, that own vocalization skills should be a prerequisite for sensorimotor activity related to action verbs, if vocalization is the key factor that drives sensorimotor activity. In our sample, the two age groups differed in terms of their expressive vocabulary for the three verbs we used. This means that, in our sample, very few 18-month-olds vocalized the verbs we presented, whereas a substantial number of 24-month-olds did. If mu suppression in response to action verbs were merely due to imagined vocalization, we would observe a difference between the age groups, which was not the case. Thirdly, there are to date several studies investigating the somatotopic distribution of sensorimotor activity associated with action verbs. These studies, in adults and preschoolers (Hauk et al., 2004; James & Maouene, 2009), indicate that the activation pattern is associated with the limb one would use to perform the action described by the verb. If the sensorimotor activity associated with action verbs could exclusively be explained by heard and simulated vocalization, we would not expect to see a somatotopic distribution of sensorimotor activity. In fact, the topographies rather correspond to the location of the effector limb on the homunculus than to the location of the mouth area. In summary, our results suggest that the processing of action verbs, thus of linguistic action representations, is associated with sensorimotor involvement.

4.1.2 Action observation

The processing of observed actions, thus visual action representations, is a topic that has received much attention in recent years. Like many other studies on infants and toddlers (Nyström et al., 2011; Southgate et al., 2009; Southgate, Johnson, Karoui, & Csibra, 2010; Warreyn et al., 2013; Yoo et al., 2016), we show that toddlers of 18 and 24 months of age activate their sensorimotor system during the processing of observed actions. More specifically, we found a right-lateralized pattern of activity. Additionally, we found that the observation of means-end actions was associated with occipital activity that was slightly more pronounced in the younger age group (marginal significance). This means that there are two characteristics to discuss: the lateralization of the central activity towards the right hemisphere and the occipital activity that differs between age groups.

First, we assume that the lateralization towards the right hemisphere is associated with the modality of presentation. In our paradigm, we always presented the means object on the left side of the screen. In our video clips, the means object was always grasped ipsilaterally with the right hand. It might be the case that the toddlers mentally performed the action from their own perspective, but still with an ipsilateral grasp. To do so, they would use their left hand, which would in turn lead to a strong right-central response. This assumption is difficult to verify, since there is not much literature that is suitable for comparison. Other studies either did not include hemisphere as a factor in their analysis or they did not specify which hand grasped for the object, and nor where the object was placed (Marshall et al., 2011; Nyström et al., 2011; Warreyn et al., 2013). However, one study provides evidence in favor of our assumption. Southgate and colleagues (2009) used live presentation, where the actress's hand always entered the stage from the right side to grasp for an object on the stage. This study showed a significant suppression of the mu rhythm in the left hemisphere only (Southgate et al., 2009). This means that it could be crucial for the lateralization of mu suppression where in the visual field the first movement happens. In the case of Southgate et al.'s (2009) study the movement happened in the right visual field, which was associated with left central activity. In analogy, in our study, the first movement happened in the left visual field and was associated with right central activity. Future studies could investigate this matter by including visual field as an experimental factor.

Second, we found very strong occipital alpha suppression associated with action observation that was numerically stronger in the younger age group. Since the literature postulates that mu rhythm suppression requires the independence of occipital alpha suppression (Cuevas et al., 2014; Marshall & Meltzoff, 2011), it is important to discuss this occipital effect we observed. Our findings are in line with a study involving 9- and 12-month-olds that showed very strong occipital effects in response to observed actions, which were also stronger for the younger age group (Yoo et al., 2016). In contrast to our study, the 9- and 12-month-olds showed even stronger occipital activity than central activity. The authors state that the strong occipital effects stem from a high degree of attention allocation, which is even stronger in the 9-month-olds (Yoo et al., 2016). Despite this study mirroring our findings, we are aware of the fact that the neural activity we found is not specific to central sites as stated in literature of best practices regarding studies on the mu rhythm (Cuevas et al., 2014; Hobson & Bishop, 2016; Marshall & Meltzoff, 2011).

4.1.3 Action verbs and observed actions

On the basis of our results, it is difficult to determine whether action verbs are associated with the same sensorimotor activity as observed actions. This is because of the different lateralization that we found for action verbs and observed actions. Action verbs were associated with left central activity, whereas observed actions were related to right central activity. The right central activity for the observed actions was stronger than the right central as well as the left central activity for action verbs. Our findings are therefore similar to a study in adults, which reported stronger sensorimotor activity for observed actions than for action verbs (Moreno et al., 2013).

Despite the different lateralization for the two conditions, we found sensorimotor activity during both conditions. Our findings thus demonstrate that the sensorimotor system of 18- and 24-month-olds is involved in the processing of action verbs and observed actions. This provides evidence that the sensorimotor system is involved in the processing of different types of action representation early on in the process of verb acquisition. It further suggests a neural interrelation between action and language in toddlers, since our results showed that action and language share the sensorimotor system for their processing. Our findings extend the evidence for a language-action interrelation from behavioral and eye-tracking studies in toddlers, in which it was shown that toddlers anticipate action goals faster if they are presented with the verb beforehand compared to no verb presentation (Gampe & Daum, 2014). Furthermore, a study linking eye-tracking and transcranial magnetic stimulation (TMS) measures suggested that anticipatory gaze shifts, as measured in Gampe and Daum (2014), are associated with the suppression of the mu rhythm in adults (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013). The current study corroborates the evidence from these two studies that the interrelation of action and language is characterized by the involvement of the sensorimotor system in the processing of both domains of action representation.

4.2 Differences in mu suppression for action verbs and pseudoverbs?

Similar to previous research with adults (Buccino et al., 2005; Fargier et al., 2012; Moreno et al., 2013; Repetto et al., 2013), our results revealed a distinct sensorimotor activation in response to action verbs compared to other types of verbs. More specifically, our results showed that 18- and 24-month-olds activate their sensorimotor system during the processing of action verbs. For pseudoverbs, the sensorimotor system is just as involved as in the baseline ("I"). Most studies in adults used abstract verbs such as "to think" to contrast action verbs (Buccino et al., 2005; Moreno et al., 2013; Repetto et al., 2013), which is different from the contrast with pseudoverbs that we used. However, one study with adult participants indicated that the sensorimotor system was only involved in the processing of pseudoverbs after an associative training in which pseudoverb-action associations were formed (Fargier et al., 2012). This fits our results, which indicate that pseudoverb processing did not involve sensorimotor activity. This seems feasible, since the pseudoverbs were completely unfamiliar and no training preceded the presentation. In the current study, the difference between the neural processing of action verbs and pseudoverbs was only evident in the left central cluster, where sensorimotor activity was present for action verbs but not for pseudoverbs. Again, this lateralization could be due to the processing of linguistic action representations or due to imagined action execution. Very importantly, the difference in activity between action verbs and pseudoverbs in the left central area speaks against the assumption that sensorimotor activity during verb processing is merely associated with heard vocalizations.

Further, our results indicate that both action verbs and pseudoverbs are associated with occipital activity. Importantly, occipital activity did not differ between the two conditions. As discussed above (in 4.1.2), this could be due to attentional or processing demands. There are two possible explanations for these occipital effects, which are equally pronounced in both action verbs and pseudoverbs. In the following, we first offer a more low-level interpretation of this result, followed by a more high-level one. First, we have to consider that our baseline, which served to calculate the ERD scores, contained a linguistic stimulus, namely the "I". This stimulus, in contrast to the action verb or the pseudoverb, is monosyllabic. It is possible that disyllabic stimuli as our action verbs (e.g., "schnii-de") and pseudoverbs (e.g., "schraa-de") require a higher amount of overall processing than monosyllabic stimuli (e.g., "Ich"), which could be associated with a decrease in occipital alpha during the second acoustically presented word ("cut") compared to the first ("I"). Second, the action verbs and pseudoverbs were embedded in a sentence structure. The sentences always started with “I”, which was followed by the action verb or the pseudoverb. The “I” might have served as a cue creating expectancy that something important might follow within the sentence structure. This expectancy could be associated with allocation of attention.

In summary, our results show that the sensorimotor system reacts only to action verbs, which have a motor-related meaning, but not to pseudoverbs that are unfamiliar. This means that, similar to research in adults (Moreno et al., 2013; Rüschemeyer et al., 2007), our findings support the hypothesis that action verbs that are strongly motor-related involve sensorimotor processing.

4.3 Age differences in mu suppression in response to verbs?

The third main question of the current study was whether 18- and 24-month-olds differ in terms of sensorimotor involvement during verb processing. Our results indicate that there is no difference in sensorimotor processing of action verbs between the two age groups. In the introduction, we proposed two factors that could influence whether the sensorimotor processing of verbs differs or not: Expressive verb repertoire and motor experience. Expressive verb repertoire was assumed to be different between the two age groups (Golinkoff & Hirsh-Pasek, 2008; Kauschke, 2012). The results from our parent questionnaire support this assumption. The 18-month-olds vocalized the action verbs we used in our paradigm significantly less often than the 24-month-olds. If the children’s expressive vocabulary influences the sensorimotor processing of verbs, one would expect a differential sensorimotor processing of verbs in the two age groups, which was not the case in the present study. With respect to motor experience, the age groups tested in the present study were not expected to differ because we used very basic means-end actions. The results from the parent questionnaire support this assumption. Both age groups had enough opportunity for associative learning with respect to mapping particular verbs onto particular actions.

Therefore, if motor experience were the factor that drives differences in sensorimotor processing of action verbs, we would not expect to find differences between the age groups. Indeed, our results indicated that the two age groups did not differ with respect to the involvement of the sensorimotor system during action-verb processing. Accordingly, expressive verb repertoire is probably not a main factor that influences the sensorimotor processing of verb at this young age. However, it is possible that the parent questionnaire we used was not comprehensive enough and a broader measure of overall expressive vocabulary would be associated with differences in sensorimotor verb processing between the age groups. In future studies, language status should be tested in greater detail because previous studies linked expressive vocabulary size to toddlers' prediction of the continuation of a heard sentence (Mani et al., 2016; Mani & Huettig, 2012).

Furthermore, we assumed that first-hand motor experience could be associated with the processing of verbs. In our study, both age groups were familiar with the actions we presented, as indicated by the caregivers. Also, both age groups processed the action verbs in a similar way, which fits the result that both age groups are equally familiar with the actions. However, as regards the language questionnaire, our measure of motor experience might not have been sensitive enough to detect possible differences. We only asked the caregivers to indicate whether or not the toddlers performed the actions during playtime. Future studies could include other measures of motor experience by including standardized action execution trials for all toddlers, or perhaps a test battery to account for fine-motor skills. Furthermore, motor experience could be experimentally manipulated in a verb-learning paradigm, which would be especially interesting in terms of the associative learning hypothesis (Cooper et al., 2013).

4.4 Future considerations

There are at least three issues that need further attention in future studies. Firstly, since there were strong occipital effects for all conditions in the current study, future studies should carefully include occipital electrode clusters in their analysis (Cuevas et al., 2014). Secondly, there were lateralized central effects in the current study. This makes comparisons between the processing of action verbs and observed actions very difficult. Future studies should consider balancing the location of the means object during presentation, in order to obtain bilateral sensorimotor activity for observed actions. Alternatively, the location of the means object could be experimentally manipulated, which would provide information about the role of the object location in sensorimotor processing of actions. Finally, future studies could include more comprehensive measures of language status and motor experience in order to investigate their role in sensorimotor action-verb processing. Also, a learning paradigm in which pseudoverbs are linked to unfamiliar actions could be fruitful for studying the role of the type of motor experience (first-hand, observational) on verb processing and the associated sensorimotor involvement.

5. Conclusion

The present study showed that the sensorimotor system of toddlers is activated during the processing of action-related verbs. As in adults, the sensorimotor involvement was distinct for familiar action verbs compared to pseudoverbs in toddlers at 18 and 24 months of age. This means that the sensorimotor system is already involved in the processing of action verbs at the beginning of verb acquisition. The comparison with the processing of observed actions indicates that the sensorimotor system underlies both action-verb and action processing. This suggests that the two different types of action representation, linguistic and visual, are interrelated on the neural level, since they share the sensorimotor system as their common processing system.

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B) Study 2: Action verbs facilitate sensorimotor prediction of observed actions in toddlers

A similar version of this study has been submitted to *Developmental Cognitive Neuroscience:* Antognini, K., Hauser, S., & Daum, M. M. (submitted). Action verbs facilitate sensorimotor prediction of observed actions in toddlers. *Developmental Cognitive Neuroscience*.

Abstract

Throughout development, the sensorimotor system is involved in making predictions derived from action language and observed actions. It is likely that language and action processing affect each other within this common processing system. Indeed, action verbs facilitate toddlers' action predictions measured by predictive gaze shifts, which are causally related to sensorimotor activity in adulthood. However, it is not yet clear whether the sensorimotor system is involved in this facilitation in toddlers. Therefore, the current study investigated if action verbs affect the sensorimotor processing of observed actions in 24-month-olds. We presented sentences comprising an action verb or a neutral expression, and subsequently video clips of the corresponding means-end action. To assess sensorimotor activity, we measured power changes of the mu rhythm, using electroencephalography (EEG). Results showed that the sensorimotor system was more active during the processing of an observed action after the toddlers had listened to an action verb, compared to a neutral expression. The current finding suggests that action verbs activate the sensorimotor system through which action prediction is facilitated.

Keywords: mu rhythm, EEG, action prediction, predictive coding, mirror neuron system

1. Introduction

Language and actions are essential to human social interactions (Tomasello, 2001), in which we constantly predict the behavior of our interaction partners (Gredebäck & Falck-Ytter, 2015). These predictions are observed both within the domains of actions (Daum & Gredebäck, 2011; Daum, Vuori, Prinz, & Aschersleben, 2009; Falck-Ytter, Gredebäck, & von Hofsten, 2006), and language (Mani, Daum, & Huettig, 2016), as well as across these two domains (Gampe & Daum, 2014; Springer & Prinz, 2010). Based on these and similar findings, actions and language are assumed to target a common neural processing system (Rizzolatti & Craighero, 2007). The human sensorimotor system is a potential candidate for this common processing already early in development (Antognini & Daum, 2017). However, how exactly predictions in the action and language domains interact and influence each other, especially early in life, is not well described. Therefore, in the current study, we investigated toddlers' sensorimotor processing of observed actions in the context of action language to examine how action language influences the neural processing of observed actions.

Across the lifespan, an observer's sensorimotor system contributes to the neural processing of observed actions (Liao, Acar, Makeig, & Deak, 2015; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Warreyn et al., 2013). This suggests that a similar neural system is used to produce actions as well as to process observed actions in order to predict forthcoming actions (Kilner, Friston, & Frith, 2007a). The predictive coding account proposes a theoretical model which states that the sensorimotor system is involved in action prediction by predicting the most probable motor program used to attain the action goal, based on past experience (Kilner et al., 2007a). Empirical evidence corroborates this assumption by showing that the sensorimotor system is already active before any movement in an action sequence is observable (Southgate, Johnson, Karoui, & Csibra, 2010; Southgate, Johnson, Osborne, & Csibra, 2009). This shows that visual information about the action and its context is used for action prediction in the sensorimotor system. However, social interactions offer also other action-related information, which could feed into the action-prediction process, for instance, sounds and action language.

Indeed, sounds that are associated with actions, elicit sensorimotor activity as well (Paulus, 2012; Paulus, Hunnius, & Bekkering, 2013; Pineda et al., 2013), especially if they are related to first-hand experience with producing the action that elicits the sound (Gerson, Bekkering, & Hunnius, 2015). Furthermore, the sensorimotor system of adults, children and toddlers is involved in processing action-related language (Antognini & Daum, 2017; James & Maouene, 2009; Moreno, de Vega, & León, 2013). More specifically, action verbs (i.e., describing observable activities) are associated with sensorimotor activity, in contrast to other types of verbs that are either abstract (e.g., existing, believing) or entirely novel, such as pseudoverbs (Antognini & Daum, 2017; James & Maouene, 2009; Moreno et al., 2013). This finding suggests that action verbs are potentially used in the action prediction process, because they activate the sensorimotor system similar to visual action information. How action and language input can feed into these predictions is illustrated in the following example. Imagine a situation in the kitchen where a parent verbalizes what he or she is about to do: "Now, we have to cut this carrot into pieces". Subsequently, the toddler observes how the parent is cutting a carrot into pieces. First, the toddler can make observation-based predictions (Daum, Prinz, & Aschersleben, 2008, 2009; Luo & Johnson, 2009; Woodward, 1998) using the sensorimotor system (Southgate et al., 2009). Second, the toddler can derive two kinds of predictions based on the language input: *communicative* and *referential predictions* (Fischer & Zwaan, 2008). Communicative predictions are predictions of what is going to be said next (Fischer & Zwaan, 2008). For example, the toddler can predict from the first part of the sentence "Now, we have to cut this carrot into…" that a noun, which fits the meaning of the sentence, has to follow. Already two-year-olds make such predictions, that is, they shift their gaze to the picture of a cake, after having heard the verb “eat” (Mani et al., 2016). Thus, communicative predictions act within the language domain. In contrast, referential predictions anticipate from the language input, what is going to happen next in the action domain (Fischer & Zwaan, 2008). Therefore, they act across domains. This means that the toddler can predict the parent’s next action steps after having heard the sentence “Now, we have to cut this carrot into pieces”. It has been suggested that, similar to observation-based predictions, the sensorimotor system is involved in making referential predictions (Fischer & Zwaan, 2008). If referential and observation-based predictions both involve the sensorimotor system, it is plausible that they also interact with each other within the sensorimotor system. One goal of the present study was to measure how a congruent referential communicative input influences the observation of a subsequent observed action sequence.

A number of behavioral studies in adults and toddlers have investigated this possible interaction between language and action. Springer and Prinz (2010) showed that reading a verb facilitated predicting the continuation of transiently occluded actions. Adults committed fewer errors in predicting the action continuation after reading a verb, especially dynamic action verbs (e.g., running), as compared to reading a noun that was not action-related (Springer, Huttenlocher, & Prinz, 2012; Springer & Prinz, 2010). This indicates that action language, especially when describing goal-directed dynamic actions, facilitates action prediction. A similar study in infants and toddlers used eye tracking to assess the influence of action verbs on action prediction (Gampe & Daum, 2014). Action prediction was measured by predictive gaze shifts, which are eye movements towards the means object of the observed action before the actor’s hand in the video clip grasped the means object. Results demonstrated that previously presented action verbs facilitated action prediction of means-end actions. However, this facilitation was only found in 24-month-olds, but not in 12- and 18-month-olds. The authors concluded that a facilitation of action prediction induced by action verbs depends on the expressive vocabulary of the toddlers, that is, on experience with using action-language (Gampe & Daum, 2014). In line with this, a study in 14-month-olds, who have a highly restricted expressive vocabulary, demonstrated that a narrative which was presented simultaneously with the action reduced predictive gaze shifts (Sciutti, Lohan, Gredebäck, Koch, & Rohlfing, 2016).

Despite the behavioral evidence showing beneficial effects of action language onto action prediction in the case of expressive action-language experience, it remains unclear whether the action and language domain interact with each other within the sensorimotor system already early in development. Previous studies demonstrated that toddlers' sensorimotor system process action verbs and observed actions presented in isolation (i.e., verbs without observational input, observed actions without language input Antognini & Daum, 2017). However, the question remains, whether the two domains interact neurally when inputs from both domains co-occur. Therefore, the current study investigated whether auditorily presented action verbs induce sensorimotor activity, which facilitates subsequent action prediction in toddlers.

We presented 24-month-old toddlers with sentences comprising either dynamic action verbs (e.g., "I'll show you cutting") or neutral expressions ("I'll show you something"), to trigger referential predictions. After each auditorily presented sentence, the toddlers observed a video clip of a corresponding means-end action. Using electroencephalography (EEG), we assessed sensorimotor activity during action observation depending on the sentence the toddlers had previously heard. Sensorimotor activity was measured by changes in the power of the mu rhythm. The mu rhythm is an alpha rhythm occurring over central regions of the scalp with the property that the amplitude, thus the power, decreases when the sensorimotor system is active (Pfurtscheller, 1992). The mu rhythm is topographically and functionally similar in adults, children, toddlers, and infants (Marshall & Meltzoff, 2011) and therefore a suitable measure to assess sensorimotor activity throughout development (Fox et al., 2016).

The following hypotheses guided our research: First, in line with previous findings (Antognini & Daum, 2017), we expected that action verbs are associated with a suppression of the mu rhythm. Second, we expected that the power of the mu rhythm is lower for observed actions that were preceded by action verbs, compared to observed actions that were preceded by a neutral expression. This hypothesis is based on findings that action verbs were associated with a facilitation of predictive gaze shifts during actions (Gampe & Daum, 2014), that predictive gaze shifts are related to the activity of the sensorimotor system (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013), and that the sensorimotor system serves action prediction (Southgate et al., 2010). Accordingly, action verbs feed into the action-prediction process by pre-activating the sensorimotor system.

2. Materials and Methods

2.1 Participants

The final sample included 32 toddlers (17 female) between 23 and 24 months of age (M = 728.8 days, range = 705-751 days). An additional 12 toddlers (5 female) were tested but excluded because of refusal during the application of the EEG sensor net (n = 5), experimenter error (n = 1), or failure to reach a minimum of 2 artifact-free trials per experimental condition (n = 6). Using a low trial criterion is common practice in EEG studies with infants and toddlers (de Klerk, Johnson, Heyes, & Southgate, 2015; Southgate et al., 2009). Toddlers were recruited from a database of parents who volunteered to participate in infant and toddler studies. All toddlers were born full term (gestation ≥ 37 weeks, birth weight ≥ 2500 g) and grew up in monolingual Swiss German households. Caregivers gave informed written consent, and the study was approved by the local ethics committee, in accordance with the 1964 Helsinki declaration and its later amendments. As compensation for their participation, the toddlers received an age-appropriate toy (value equivalent to 5 USD) and a certificate of participation with a photograph of themselves.

2.2 Stimulus material

We used auditory and visual stimuli. The auditory stimuli consisted of ten prerecorded audio files with sentences spoken by two Swiss-German native speakers. We chose two speakers to enhance the variability in the auditory stimuli, because greater stimulus variability in auditory stimuli increases the processing of words in toddlers (Rost & McMurray, 2009). One female and one male speaker narrated five of the sentences, respectively. Four sentences belonged to the verb condition and one sentence to the neutral condition. All sentences started with „Ich zeig dir“ [I’ll show you] (0-900 ms), followed by a verb (verb condition) or by a neutral expression (neutral condition) from 950-1650 ms. We used four different familiar, early-acquired action verbs (Szagun, Stumper, & Schramm, 2009): „maale“ [drawing], „schniide“ [cutting], „baue“ [building], and „zuemache“ [closing]. The neutral expression was „öpis“ [something].

The visual stimuli consisted of four different video clips depicting the means-end actions, which corresponded to the action verbs: drawing a spiral on a piece of paper, cutting a toy carrot into three pieces, building a tower with three building blocks, and closing the lid of a jar. Each video clip showed the torso, arms, and hands of a female actress, who sat at a table. Two objects were on the table in front of the actress. The position (left, right) of the means object (pencil, toy knife, building block, lid) and the goal object (paper, toy carrot, two building blocks, jar) were counter-balanced. Each video clip showed the same action steps (see Fig.1): First, the actress sits at the table with her hands in a resting position (0-400 ms). Then, she lifts her hand to reach and grasp the means object ipsilaterally (400-1640 ms). Depending on the position of the means object, the actress uses her right or her left hand. The means object is transported to the goal object (1640-2880 ms), whereupon the appropriate action is performed (2880-4120 ms). After completing the action, the actress returns her hands to the resting position. The total duration of the video clip was either 6000 ms for actions without a tool object to perform the action (building and closing), or 7000 ms for actions with a tool object to perform the action (drawing and cutting). This variability was caused by the fact that, in videos with a tool object, the actress had to place the tool object on the table before returning her hands to the resting position.

2.3 Procedure

On arrival, the caregivers completed a language questionnaire that asked which verbs, out of one hundred, the toddler actively produced in daily life (i.e., spontaneous utterance and consistent use to describe an action). The language questionnaire was adapted to Swiss German from the German version of the McArthur CDI (Szagun et al., 2009).

EEG was measured in a sound-attenuated, electrically shielded, and dimly lit room. The toddler sat on the caregiver's lap about 60 cm from a 17-inch screen with adjacent loudspeakers. For stimulus presentation, we used Psychtoolbox (version 3.0.11) in MATLAB R2013a. A white fixation dot appeared on the screen for 1000 ms as between stimulus interval (BSI). Each trial started with an acoustically presented sentence. This sentence either contained one of the four action verbs (verb condition) or the word "something" (neutral condition). During the sentence presentation, no visual stimulus was visible. Immediately after the sentence presentation, a video clip of an action was shown. In the verb condition, the action was congruent to the verb in the sentence. In the neural condition, one of the four actions was presented randomly (see Fig. 1). Trials were presented in 8 separate blocks of 16 trials each (4 female speaker/verb, 4 male speaker/verb, 4 female speaker/neutral, 4 male speaker/neutral). A one-minute play break followed each block. Stimulus presentation was terminated when the toddler was no longer attentive, or when the maximum of 8 blocks was reached. The toddlers were monitored by video cameras from lateral and front view. If the toddler moved or did not look at the screen, the experimenter manually released the presentation of an attention grabber (video of bouncing cube with sound effect).

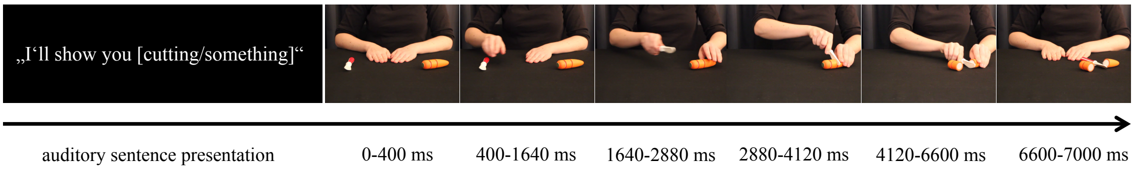

Fig. 1. Structure of one experimental trial. As an example, the action *to cut* is depicted, which was preceded by either the corresponding action verb or a neutral expression. The structure was analogous for the other three actions used in the paradigm.

2.4 EEG recording and analysis

The EEG was recorded at 500 Hz sampling rate using a 128-electrode HydroCel sensor net (EGI, Eugene, OR, USA) and a NetAmps 300 amplifier (EGI, Eugene, OR, USA). Online, data were referenced to the vertex electrode (Cz) and high-pass filtered at 0.1 Hz. Impedances were kept below 50 kΩ. Offline preprocessing was performed in the EEGLAB toolbox (Delorme & Makeig, 2004). Data were band-pass filtered between 0.3-30 Hz. Bad electrodes were removed after visual inspection. Furthermore, the outermost electrodes were removed due to insufficient contact to the scalp. An independent component analysis (ICA) was performed to remove artifacts due to eye blinks, saccades, sweating, and heart beat (Delorme & Makeig, 2004). Missing channels were interpolated with a spherical interpolation algorithm, and data were rereferenced to common average reference.

Continuous EEG data were segmented into epochs containing the sentence presentation as well as the video presentation. Epochs lasted from -1000 ms before and 6400 ms after sentence onset. We chose these epochs to ensure that we analyzed EEG trials for which the toddler attended the sentence and the video attentively and quietly. Trials in which the toddlers moved or did not look at the screen, were removed from further analysis. On average, the toddlers provided 11.9 artifact-free trials for the verb condition (range 2-26) and 10.8 artifact-free trials for the neutral condition (range 2-33).

The segmented data was analyzed in Matlab (R2014b) applying a wavelet analysis with 7 cycles between 4 and 20 Hz. The frequency band of interest was defined between 6 and 10 Hz, which corresponds to the mu band in toddlers that peaks at 8 Hz for 24-month-olds (Berchicci et al., 2011). We calculated event-related desynchronization (ERD) values according to Pfurtscheller (2001). As baseline we selected the period during sentence presentation in which "I'll show you" (0-900 ms after verb onset) was presented. Event-related desynchronization was calculated for the period during sentence presentation in which the verb or the neutral expression was presented (950-1650 after verb onset; verb time-window), as well as for the period of video presentation in which the grasp towards the tool object could be observed (0-1640 ms after video onset; grasping time-window). The grasping time-window was based on the time window chosen by Gampe & Daum (2014). Within the frequency band and time windows of interest, we selected three different clusters. We chose a left (E30, E31, E36, E37, E42, E53, E54) and right (E79, E80, E86, E87, E93, E104, E105) centro-parietal electrode cluster. To account for potential attentional effects, we additionally selected an occipital electrode cluster (E66, E69, E70, E71, E74, E75, E76, E82, E83, E84, E89). Statistical analyses were performed in the R statistical package (R Core Team, 2017).

3. Results

3.1 Mu suppression for action verbs

First, we analyzed whether listening to an action verb resulted in more mu suppression than listening to a neutral expression. Mu suppression in response to action verbs has been shown to be present by 18 months of age (Antognini & Daum, 2017). To make sure that toddlers know the action verbs, we included only toddlers who had all four verbs in their expressive vocabulary ($N = 17$). To account for the dynamics in power change of the mu rhythm (as suggested by Fox et al., 2016), we applied one paired t-test per time point ($n = 350$) on the ERD values [%] of the mu frequency band (6-10 Hz) within the verb time-window (950-1650 ms after sentence onset) to compare the verb condition and the neutral condition. Since the tested power values within the time window were continuous, and therefore not independent from each other, we applied Fisher's Omnibus test with permutation statistics (iterations $N = 10'000$) as suggested by Potter and Griffiths (2006). With this procedure, the p-values from the single t-tests are combined into an overall p-value with Fisher's function (Fisher, 1932). Results indicated a significant difference in ERD between the verb ($M = -4.10$, $SD = 3.72$) and the neutral expression ($M = -3.79$, $SD = 1.41$), in the left centro-parietal cluster, $\chi^2(N = 17) = 1392.72$, $p < .001$. In the other electrode clusters conditions did not differ significantly: right centro-parietal, $\chi^2(N = 17) = 333.67$, $p = 1$, occipital, $\chi^2(N = 17) = 378.57$, $p = 1$.

For the following to reasons, we ran an exploratory analysis on the toddlers who did not have all four verbs in their expressive vocabulary ($N = 15$): First, it is possible that toddlers react differently to the presentation of action verbs and neutral expressions depending on their expressive vocabulary (Gampe & Daum, 2014). Second, it has been suggested that sensorimotor activity is experience-dependent (Kilner et al., 2007a; Kilner, Friston, & Frith, 2007b). For this group of toddlers, ERD did not differ between conditions in any of the electrode clusters; left centro-parietal, $\chi^2(N = 15) = 273.36$, $p = 1$, right centro-parietal, $\chi^2(N = 15) = 726.649$, $p = .239$, occipital, $\chi^2(N = 15) = 324.15$, $p = 1$.

3.2 Difference in mu power during action observation

Second, we analyzed mu suppression in the grasping time-window. Analysis was identical to the verb-time-window, except for the number of time points analyzed ($n = 821$). For the group of toddlers with all verbs in their expressive vocabulary, results indicated a significant difference in ERD during the observation of grasping between the verb condition ($M = -5.73$, $SD = 5.45$) and the neutral condition ($M = -4.36$, $SD = 5.02$), in the left centro-parietal cluster, $\chi^2(N = 17) = 2172.81$, $p < .001$ (see Fig. 2). In the other electrode clusters, conditions did not differ significantly: right centro-parietal, $\chi^2(N = 17) = 1279.25$, $p = 1$, occipital, $\chi^2(N = 17) = 1605.27$, $p = .738$. For the group of toddlers who did not have all four verbs in their expressive vocabulary, ERD did only differ in the occipital electrode cluster, occipital, $\chi^2(N = 15) = 1880.39$, $p < .001$, such that ERD was greater in the verb condition ($M = -9.88$, $SD = 4.10$) compared to the neutral condition ($M = -6.49$, $SD = 4.58$). The centro-parietal clusters did not reveal any significant condition differences, left centro-parietal, $\chi^2(N = 15) = 715.87$, $p = 1$, right centro-parietal, $\chi^2(N = 15) = 1107.70$, $p = 1$.

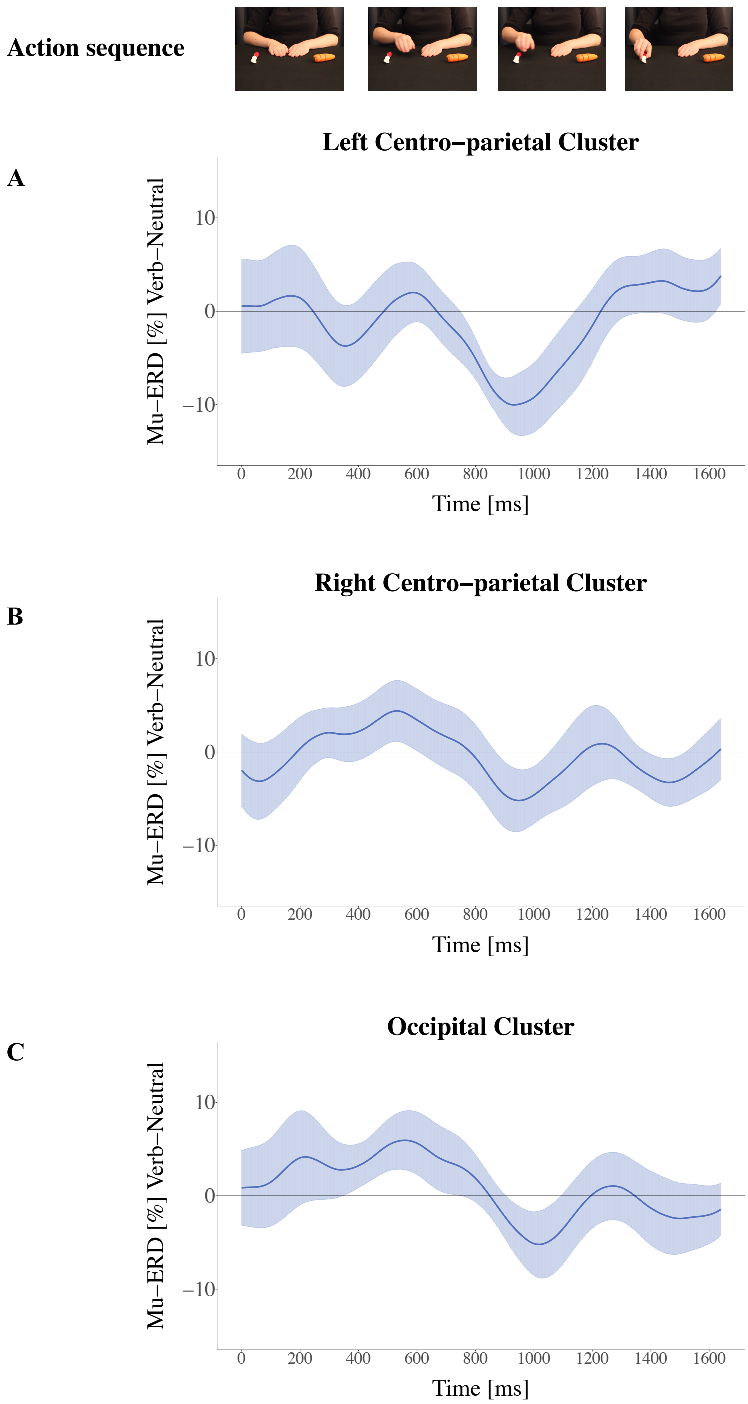

Fig. 2. Condition difference (verb – neutral) ERD of mu power [%] during action observation for toddlers (N = 17), who have all four verbs in their productive vocabulary. Panel A displays continuous mean difference (± 1 *SE*) in the left centro-parietal cluster within the time window, in which the grasp for the means object was observable in the video clip. Panel B depicts the mean difference for the right centro-parietal and Panel C the occipital cluster.

4. Discussion

To better understand the underlying mechanisms of how action verbs facilitate action prediction already early in development, we investigated whether action language affects sensorimotor activity during action observation in toddlers. We presented 24-month-olds with a spoken sentence followed by a video clip of an action. The sentence either contained an action verb (e.g., “I’ll show you cutting”; verb condition) or a neutral expression (e.g., “I’ll show you something”; neutral condition). In the video clip, a means-end action was presented which, in the verb condition, corresponded to the action verb (e.g., cutting a carrot into pieces). Sensorimotor activity was assessed by EEG, measuring the suppression of the mu rhythm, an indicator for action prediction (Kilner et al., 2007a; Southgate et al., 2010). Our results show that action verbs are associated with more sensorimotor activity than neutral expressions, but only in 24-month-old toddlers who have these verbs in their expressive vocabularies. Furthermore, hearing an action verb enhanced sensorimotor processing during the observation of corresponding actions in 24-month-old toddlers, who have these verbs in their expressive vocabulary. More specifically, sensorimotor activity was higher at left centro-parietal sites, indicated by a greater suppression of the mu rhythm, for visually presented actions that followed an acoustically presented corresponding verb, compared to a neutral expression. Toddlers who did not have the verbs in their expressive vocabularies only showed enhanced occipital activity during action observation after having heard an action verb.

4.1 Mu suppression during action-verb processing

We analyzed whether action verbs were associated with more sensorimotor activity than neutral expressions, since action verbs elicit sensorimotor activity in toddlers but, for instance, pseudoverbs do not (Antognini & Daum, 2017). The results showed that action verbs were associated with significantly more left centro-parietal mu suppression than neutral expressions. However, this was only true for the group of toddlers who had all these verbs in their expressive vocabularies. This result replicates the finding that the sensorimotor system of 24-month-olds is involved in processing action verbs (Antognini & Daum, 2017). Importantly, mu-suppression differences were limited to centro-parietal sites, indicating sensorimotor processing independent of differences in attention allocation (Cuevas, Cannon, Yoo, & Fox, 2014; Marshall & Meltzoff, 2011). The difference in mu suppression at centro-parietal sites was left lateralized, which is in line with previous findings indicating that action verbs are associated with left-lateralized processing (Antognini & Daum, 2017; Hauk & Pulvermüller, 2011). This left-lateralization is likely the result of an overall left dominant pattern of language processing (Knecht et al., 2000). Furthermore, the sensorimotor involvement during action-verb processing was dependent on the expressive vocabulary of the toddlers, thus their experience. This is in line with findings showing that sensorimotor activity is experience-dependent, being high for individuals with high expertise and lower for individuals with intermediate expertise (Liew, Sheng, Margetis, & Aziz-Zadeh, 2013). However, it stands in contrast with findings indicating that expressive verb knowledge is not necessary for action verbs to elicit sensorimotor activity (Antognini & Daum, 2017). Importantly, Antognini and Daum (2017) used a slightly different language questionnaire, which could explain the differences with respect to the influence of expressive vocabulary on sensorimotor verb processing. In sum, the results with respect to the mu suppression during action-verb processing demonstrated that action verbs were associated with sensorimotor activity, given that the toddlers actively use the action verbs in daily life.

4.2 Action verbs facilitate action processing during action observation

The results of the current study demonstrated greater mu suppression during the observation of a goal-directed action after previous presentation of a sentence with a corresponding action verb, compared to a linguistic neutral expression. This was only the case if toddlers had all the action verbs in their expressive vocabulary. For children who did not have all presented action verbs in their expressive vocabulary, we found condition differences only at occipital sites, which we interpret as enhanced attention allocation to the observed action after hearing a congruent action verb compared to a neutral expression (Cuevas et al., 2014; Pfurtscheller, 2001). However, this group of toddlers did not reveal any modulation in sensorimotor activity elicited by the action verb, which would have been an indicator for modulated action prediction (Kilner et al., 2007a, 2007b; Southgate et al., 2009). In contrast, toddlers with all four verbs in their expressive vocabulary, revealed such a modulation in action prediction. Predictive processing of observed events has been reported before, both when observing goal directed actions (Gampe & Daum, 2014) and when making inferences about the continuation of heard sentences (Mani & Huettig, 2012). Interestingly, the time course of the difference in sensorimotor activity between the two conditions (verb, neutral) is similar to the time course reported earlier in an eye tracking study (Gampe & Daum, 2014). It showed faster predictive gaze shifts towards an action goal when the preceding sentence comprised a congruent action verb, compared to when it did not (Gampe & Daum, 2014). Thus, in the current study, as well as in Gampe and Daum's study (2014), action verbs facilitated subsequent action processing, indicated by enhanced mu suppression or faster predictive gaze shifts, respectively. However, we still need to be cautious about making strong claims on the relation between predictive gaze shifts and mu suppression on the basis of our data, because we do not have eye-tracking data from the toddlers we tested. Future studies with simultaneous assessment of neurophysiological and eye-tracking data will help to clarify this relation (Bache et al., 2017).

Nevertheless, our results are in line with the predictive coding account (Kilner et al. 2007a,b), which states that the sensorimotor system serves for generating predictions based on past experience, and that more precise predictions are associated with more sensorimotor activity than less precise ones: Very precise action predictions, as in the case in which the observer has high expertise, involves the sensorimotor system more than in the case in which the observer is less capable of making specific predictions, for instance, if the familiarity with an action is at a medium level (Gardner, Goulden, & Cross, 2015; Liew et al., 2013). In this line, we assume that a linguistic label that is within the observer's productive language repertoire allows for precise referential predictions of an observed congruent action. We argue that the toddlers with all four action verbs in their expressive vocabulary, thus high expertise in verb processing, made referential predictions after hearing an action verb, indicated by the enhanced mu suppression during verb presentation. The linguistic label resulted in an increased sensorimotor activity that then helped to predict the action more precisely than an observable action accompanied by a very broad and unspecific description as in the case of the neutral expression. It remains however unclear if precision on the level of semantics or on the level of manner drives this effect. On the one hand, the semantic representation of the action verb (i.e., "cutting") is much more specific than the semantic representation of the neutral expression (i.e., "something"). On the other hand, evidence demonstrates that, although less topographically focused than in adults, sensorimotor activity associated with action verbs is somatotopically organized already in children (James & Maouene, 2009). Therefore, precision could relate to the manner in which the action is performed. The action verb describes the manner, that is, the effector-limb (e.g., hand) much more precisely than the neutral expression, which could imply any limb. Therefore, in both cases (semantics and manner), the sensorimotor activity associated with the neutral expression is less specific compared to the action verb (Liew et al., 2013). This could lead to a less specific effect of the neutral expression onto forthcoming sensorimotor activity, compared to the action verb.

Unfortunately, it is not possible to clarify which of the two mechanisms, semantics or manner, underlies the effect we demonstrated in the current paper for the following reasons. First, we did not include any action verbs describing actions executed with other limbs than the hand, which would need to be included as a control condition to verify if the underlying mechanism is based on the somatotopic distribution of sensorimotor activity elicited by the action verbs. Second, it is difficult to tell the exact source of the measured activity relying on surface measurement because it reflects a mixture of activity from various neural sources, which are hard to separate (de Haan, 2013). Third, we cannot confirm that the meaning of the verb underlies the effect, because all the action verbs we used were congruent to the actions that were subsequently observed. The neutral expression cannot be regarded as incongruent, because it does not introduce any conflict in processing. Therefore, future studies are needed to answer the question about the importance of semantic and somatotopic congruency.

Irrespective of the mechanism, which has to be studied more thoroughly in the future, auditorily presented action verbs facilitated subsequent visual action processing only in left centro-parietal sites. We interpret this left-lateralization as a consequence of the left-lateralized processing of the action verbs that were presented. It is likely that the action verb activated the sensorimotor system in the left hemisphere, as already demonstrated in adults (Hauk & Pulvermüller, 2011) and toddlers (Antognini & Daum, 2017). Under this assumption, the left-lateralized activity elicited by the action verb might have added up with the bilateral activity elicited by the action observation, resulting in an enhanced left-sided activity pattern. Such an additive effect of sensorimotor activity has been shown for simultaneous audio-visual stimuli (McGarry, Russo, Schalles, & Pineda, 2012). It is, however, important to mention that it is most probably not the communicative nature of the presented action-verb sentences, which affected the suppression of the mu rhythm during action observation, as suggested by Pomiechowska and Csibra (2017). This is because both sentences are somehow communicative in nature, but the action-verb sentence additionally directs the observer's attention very specifically to the action that is subsequently observed (Pomiechowska & Csibra, 2017). However, the specific role of communication can only be scrutinized when including a clearly non-communicative stimulus in future studies.

5. Conclusion

The present study shows that the sensorimotor system is involved in the interrelation of language and action. It demonstrates that language, specifically congruent action verbs from the expressive vocabulary, facilitates toddlers' sensorimotor action prediction during subsequent action observation. Overall, this study contributes to the understanding of the interrelation between language and action and it underlines the importance of using action language to promote toddlers' understanding of other people's actions.

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08/2014-12/2014	Student assistant, Developmental Psychology: Infancy and Childhood (Prof. Dr. Moritz M. Daum), Department of Psychology, University of Zurich, Zurich, Switzerland
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02/2013-02/2014	Clinical intern, Swiss Epilepsy Center (supervision: Prof. Dr. H. Jokeit), Zurich, Switzerland
09/2011-12/2013	Student assistant, Psychological Methods, Evaluation, and Statistics (Prof. Dr. C. Strobl), University of Zurich, Zurich, Switzerland

Publications

Antognini, K., & Daum, M. M. (2018). Effects of verb-action congruence on sensorimotor processing of goal-directed actions in two- year-olds: A technical report. PsyArXiv. https://doi.org/10.31234/osf.io/g8fu4

Antognini, K., & Daum, M. M. (2017). Toddlers show sensorimotor activity during auditory verb processing. *Neuropsychologia,* https://doi.org/10.1016/j.neuropsychologia.2017.07.022

Maffongelli, L., Antognini, K., & Daum, M. M. (2018). Syntactical regularities of action sequences in the infant brain: When structure matters. *Developmental Science,* e12682. https://doi.org/10.1111/desc.12682

Conference Talks

Antognini, K., & Daum, M. M. (2017). When verbs facilitate action-goal anticipation - the role of the sensorimotor system. Talk held at LIFE Fall Academy, Zurich, Switzerland

Antognini, K., & Daum, M. M. (2017). Toddlers show mu-suppression during auditory verb processing. Talk held at the Lancaster Conference of Infant and Child Development, Lancaster, United Kingdom.

Ledergerber, K., & Daum, M. M. (2016). How the sensorimotor system helps toddlers to grasp the idea of action language. Talk held at the LIFE Fall Academy, Berlin, Germany.

Poster Presentations

Hauser, S., Antognini, K., & Daum, M. M. (2018). Verben erleichtern die Handlungsverarbeitung bei Kleinkindern: Eine EEG Studie im Mu- und Beta-Frequenzbereich [Verbs facilitate action processing in toddlers: An EEG-study in the mu and beta frequency-range]. Poster presented at MaDoKo, Zurich, Switzerland

Ledergerber, K., & Daum, M. M. (2016). Action verbs are associated with sensorimotor mu-desynchronization in toddlers. Poster presented at the International Conference of Infant Studies, New Orleans, USA.

Ledergerber, K., & Daum, M. M. (2016). Action verbs are associated with sensorimotor mu-desynchronization in toddlers. Poster presented at the LIFE Spring Academy, Charlottesville, USA.

Ledergerber, K., & Daum, M. M. (2016). Differential impacts of action language on action prediction in infants and toddlers. Poster presented at the Lancaster Conference of Infant and Child Development, Lancaster, United Kingdom.

Ledergerber, K., & Daum, M. M. (2015). Turning words into actions: The early development of a sensorimotor representation of action language. Poster presented at the LIFE Fall Academy, Schloss Marbach, Germany.

Ledergerber, K., Kurthen, I., & Daum, M. M. (2015). A developmental perspective on the action-language link. Poster presented at the EEGLAB Workshop 2015, Sheffield, United Kingdom.

Ledergerber, K., Kurthen, I., & Daum, M. M. (2015). When pseudo verbs are no longer pseudo verbs: Language-action association fosters mu- and beta-suppression in response to pseudo verbs. Poster presented at the LiMaDoKo 2015, Zurich, Switzerland.

Ledergerber, K., Toller, G., & Jokeit, H. (2014). Your inside is out and your outside is in? An fMRI case study on the art of acting. Presented at the MNI Neuropsychology Day, Montreal, Canada.

Publications for the public

Publications:

Antognini., K., & Daum, M. M. (2018). Sprung zum Ich. Vom Zehnmeterbrett springen, in der vollen Bahnhofshalle lauthals ein Lied singen, eine Nacktschnecke ablecken: Wieso Mutproben Sinn machen [Why test of courage make sense]. *ZH. Das Magazin der Zürcher Kantonalbank, 1,* p. 29.

Ledergerber, K. (2017, June 2). Verbs link action to language. Why commenting on toddlers' actions is important for verb learning [Blog post]. Retrieved from https://bold.expert/verbs-link-action-to-language/

Media coverage:

Fuchs, M. (2018, July 11). Systematische Babys [Systematic babies]. Retrieved from https://www.news.uzh.ch/de/articles/2018/kluge_babys.html

Supervision of Bachelor's and Master's theses

Bachelor's theses:

Marion Gabi (2018): Neurophysiologische Grundlagen der frühkindlichen Handlungswahrnehmung [Neurophysiological bases of infants' action perception].

Stefanie Meier (2017): Der Einfluss der Babyzeichensprache auf die Sprachentwicklung bei Kleinkindern [The influence of baby signing on language development of toddlers].

Dominique R. Hungerbühler (2017): Zusammenhang von Handpräferenz und Sprachfähigkeiten [The interrelation of hand preference and language skills].

Clio Haniman (2015): Die Entwicklung der intermodalen Wahrnehmung. Die Verbindung des visuo-taktilen Systems als angeborene Fähigkeit oder erlernte Fertigkeit? [The development of intermodal perception. The relation of the visual and the tactile system as innate ability or learned skill?].

Master's thesis:

Sarah Hauser (2018): Zusammenhang von Handlung und Sprache: Eine EEG-Studie mit Kleinkindern im Mu- und Beta-Frequenzbereich [The interrelation of action and language: An EEG-study with toddlers in the mu and beta frequency-range].

Teaching

Fall 2017	Bachelor's seminar (Co-teaching with Lea Mörsdorf). Applied Developmental Psychology, Department of Psychology, University of Zurich
Spring 2017	Bachelor's seminar. Social-cognitive Development (Co-teaching with Stephanie Wermelinger), Department of Psychology, University of Zurich
Fall 2016	Bachelor's seminar. Applied Developmental Psychology (Co-teaching with Laura Maffongelli), Department of Psychology, University of Zurich
Spring 2016	Bachelor's seminar. Social-cognitive Development (Co-teaching with Stephanie Wermelinger), Department of Psychology, University of Zurich